BACK-CALCULATION OF THE GROWTH OF CAPELIN (MALLOTUS VILLOSUS) IN THE CANADIAN NORTHWEST ATLANTIC FROM MEASUREMENTS OF OTOLITHS

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Back-calculation of the growth of capelin (*Mallotus villosus*) in the Canadian northwest Atlantic from measurements of otoliths

by

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ABSTRACT

The otolith radius-fish length relationship in capelin is shown to take the form of an heterogonic curve with an inflexion point occurring at the size of maturity for both sexes. This relationship changes with sex, age and maturity. A linear relationship between otolith radius and fish length, as determined by regression analyses, was found to exist only within an age-group. This necessitated the use of separate equations for back-calculating the lengths of each age.

Growth curves of Trinity Bay capelin, as constructed from back-calculated lengths, indicated that male capelin grow faster than female capelin up to the age at maturity after which the growth rates remain the same. Inferences about age at first maturity of Trinity Bay capelin are made from otolith-age curves which suggest that capelin normally spawn more than once.

Growth compensation in its typical form and Lee's phenomenon are shown to exist in capelin and reasons are given for their presence. It is suggested that growth compensation in capelin is not only acquired from the growth patterns of the different age-groups but is also an inherent feature of its growth.

The method of ageing Trinity Bay capelin from otoliths is validated and the embryonic nucleus or larval check ring is described from the otoliths of larval capelin. Comparison of the otoliths of capelin from various regions of the northwest Atlantic indicates that there is a distinct decrease in the size of the first annulus from south to north.

The otolith radius-fish length relationships of capelin from various regions of the northwest Atlantic are compared by age, sex and maturity. No consistent differences were apparent except those created by local variations in growth rate and maturity.

Growth rates of capelin from the Bay of Fundy to northern Labrador are compared from otolith radius-age curves and length-at-age curves. The Bay of Fundy capelin are characterized by a fast growth rate, early maturity and small maximum size; the Labrador capelin are slow-growing, mature later and have a large maximum size; Newfoundland capelin are shown to be intermediate in growth rate. Reasons for these differences are discussed in relation to the hydrography of the area under consideration.

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I INTRODUCTION

A. Previous research on capelin in the Newfoundland area.

Due to its low priority on the commercial fishing scale, previous research on capelin in the Newfoundland area tended to be intermittent and restricted in the range of data. Among the most notable works are those by Jeffers (1931) who dealt mainly with larval development; Sleggs (1933) who concentrated on its economic biology; Templeman (1948) who investigated mainly its life history; and Pitt (1958a, 1958b) who concentrated mainly on the age, growth, distribution, spawning, and racial studies of capelin. These authors based their results mainly on beach-spawning coastal capelin caught during their brief spawning period and had only limited access to the demersal spawning capelin on Grand Bank or other offshore areas. Much additional age validation is needed (Templeman, 1968) as well as comparative information on the variations in growth of capelin in the Canadian area of the north-west Atlantic.

As part of an expanding program of research on pelagic fishes, capelin research was reinstated as part of the fish

investigations of the St. John's Biological Station in 1965. Samples of capelin have been obtained from all periods of the year and from all representative areas of the northwest Atlantic including an ample representation of the bank-spawning capelin.

The objectives of this paper are to provide comparative information on the growth patterns of capelin in the northwest Atlantic using the back-calculation technique and to validate the age readings as they are interpreted from the otoliths of capelin.

B. Review of the literature on the otolith-body relationship.

Otoliths have not been used as extensively as scales in back-calculating the growth history of fish. This is partly due to the fact that the back-calculation technique evolved from the scale method of age determination and partly because the thickness and irregularity of the otoliths of many fish preclude their use in the accurate estimation of age. In many cases where the otoliths are used in age and growth determinations they have to be ground down or cross-sectioned in order to reveal the annual rings. Furthermore, scale size is related to body size whereas otolith

size is head related and hence there are likely to be more difficulties with otoliths than with scales when otolith sizes are compared with body lengths. However, several authors have attempted to use otoliths in length-at-age back-calculations and their results relating to the otolith-body relationship can be ascribed to the four categories listed below:

1. The otolith-body relationship exhibits no correlation. Menon (1950) measured 600 otoliths of the poor cod Gadus minutus and found that there was virtually no correlation between the length of the fish and the width of the otolith, nor between the otolith width and the sex and age of the fish. He concluded that this emanated from the great thickness and mass of the otoliths.

2. The otolith-body relationship is linear. Scott (1954) found that a linear relationship adequately described the otolith-body relationship of the yellowtail flounder. However, his samples were restricted in length (20-50 cm) and sexes, ages and maturities were combined. Dzin-Gi-Jun and Popiel (1961) also found a linear relationship to exist between the otolith width and fish length of the Baltic herring. They also noted that older fish have

larger otoliths than younger fish of the same size, i.e. slow-growing fish have larger otoliths than faster-growing fish. Mio (1966) found a linear relationship between the otolith length and fish length of Gnathagnus elongatus and observed that at any particular length there is a great variability in the otolith radius.

3. The otolith-body relationship is curvilinear and isogonic in form. Southward (1962) in a study of the Pacific halibut found that the otolith radius-fish length relationship was curvilinear but that when data were transformed to natural logs a linear relationship could be obtained. Using analyses of co-variance he demonstrated that there were no differences in the form of the relationship between sexes or between areas. He tested the accuracy of his back-calculated lengths by comparing growth calculations obtained from his empirical curve with direct growth estimations obtained from the recapture of tagged halibut and found that the results concurred. Hempel (1959) and Sjoblom (1963) found a similar curvilinear relationship to exist in Baltic herring.

4. The otolith-body relationship is curved but of heterogonic form. Saetersdal (1953) could find no rectilinear relationship to

describe the otolith radius-fish length relationship of Norwegian haddock. He divided his empirical curve into two straight lines and attempted to remove the bend by transforming his data into natural logs but the bend still remained. He consequently concluded that the change in slope (inflexion point) was the result of a sudden change in the geometric rates of growth of the fish and the otolith. Since these changes are known to be coincidental with important physiological changes in the life of the organism, Saetersdal tried to correlate the size of the fish at the inflection point with the size at maturity but could not arrive at a good agreement. Hickling (1933) and Templeman (1968) found similar otolith-body relationships to exist in the hake and capelin respectively. Templeman, however, found that the inflexion point in capelin does occur at approximately the length at maturity.

Of all the otolith-body relationships, the heterogonic form is the most complicated and awkward in back-calculations because no single mathematical equation can describe it and often separation of the samples into sex, age and maturity categories must be done before any formulae can be derived.

II METHODS AND MATERIALS

A. Source of samples

The material from which this paper was derived represents a wide range of localities extending from the Bay of Fundy (Fig. 1) in the southern extreme of the northwest Atlantic to Davis Inlet, Labrador, in the northern region of the Canadian northwest Atlantic (Table I). In addition there is an adequate representation of both offshore and coastal stocks of capelin as well as the inclusion of immature, pre-spawning, spawning, and spent groups of capelin. The type of gear used to catch the capelin varied with maturity condition of the capelin. Beach-spawning capelin were caught by cast-nets with mesh sizes ranging from 1/2" to 3/4". Spawning and spent capelin on the southeast shoal of Grand Bank were caught by the research vessel A.T. Cameron using a No. 41 Yankee otter trawl with a headline length of 24 meters and a cod-end liner ranging from 1/2" to 1-1/8" in stretched mesh dimension. Pre-spawning and immature capelin from Trinity Bay were caught by the research vessel Investigator II using a No. 4 mid-water trawl with a mouth opening 6 meters square and a 1/2" liner in the cod-end. All larvae were caught with a 6-foot Isaacs-Kidd mid-water trawl. The cod-end of this trawl consisted of a 50 cm plankton net with a mesh size of 1.07 mm.

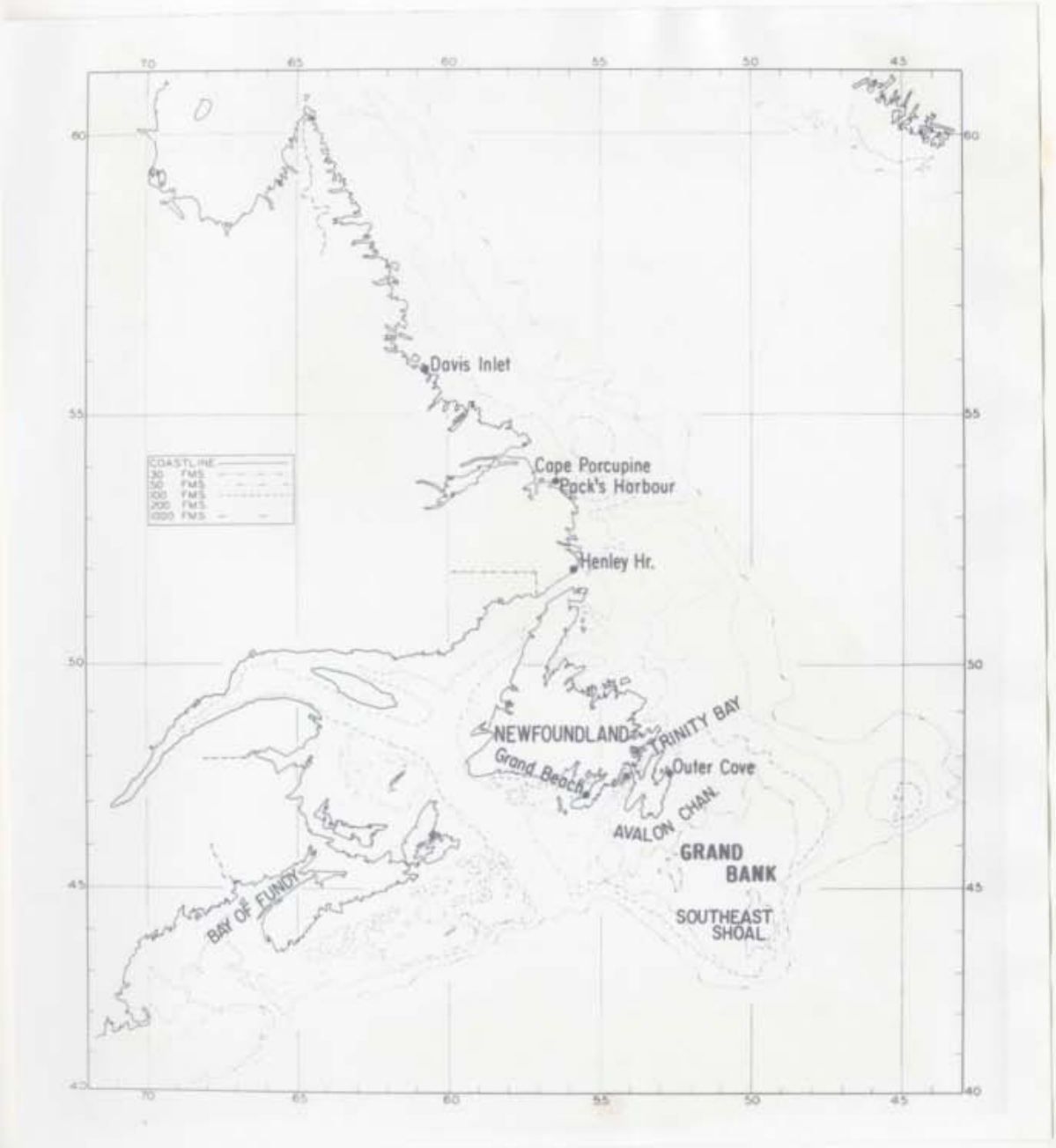

Fig. 1. Area map showing the localities and place names mentioned in the text.

B. Removing and measuring the otoliths.

The small size and high fragility of the capelin otoliths require that meticulous care must be used in their removal in order to minimize breakage. Otoliths were removed ventrally by cutting an enclave on either side of the basi-occipital bone and extracting the otoliths by means of forceps or scalpel. The otoliths were then placed in envelopes to await reading.

For ageing purposes the otoliths were placed in a glass dish with a black bottom and immersed in 95% isopropyl alcohol. The otoliths were read under reflected light using a stereoscopic model SMZ Nikon microscope with a micrometer in one eyepiece. Ages were determined from the lateral convex face of the otolith using two methods, the main method involving the alternating opaque summer bands and the translucent winter bands, and the corroborating method involving the ridge and groove method as described by Templeman (1948). All otoliths with poorly defined annuli were omitted in age determinations.

For measuring purposes the otolith was placed so that there was a vertical line extending from the rostrum to the centre of the first year (Fig. 2). Then the radius of the otolith to the outside

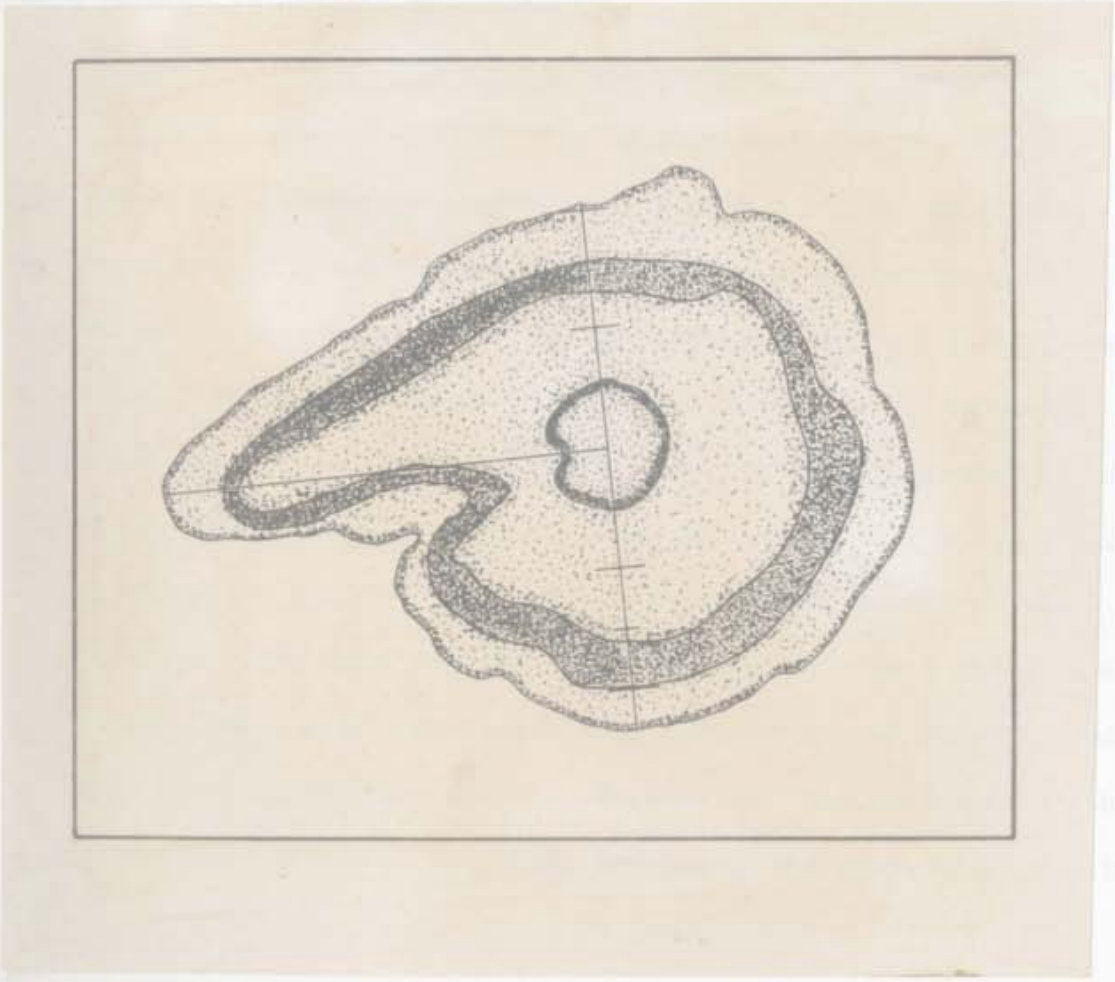

Fig. 2. Sketch of a capelin otolith indicating the manner in which the otolith radius was measured.

of each winter ring was measured by the ocular micrometer at right angles to the vertical line. As no practical purpose could be achieved by conversion to mm the otolith radii were read in terms of eye piece units (EPU). For purposes of conversion, however, 1 mm = 26.5 EPU. All otoliths with irregular or abnormal shape were omitted in otolith measurements.

C. Methods of fish measurement and conversion of preserved lengths.

For convenience and rapidity in measuring capelin, only the greatest total lengths were used, i.e. from the tip of the mandible to the end of the ventral lobe of the caudal fin deflected back in a straight line with the body. Lengths were measured in millimetres.

As many of the samples were frozen, either dry or in brine, it was necessary to determine the shrinkage factor for conversion of thawed lengths to fresh lengths. Consequently, two samples of capelin of approximately 100 fish each were measured fresh, tagged in two separate bags, one empty and the other containing brine. These were then frozen for a week after which they were thawed out in water and measured again by the same person. Regression lines of fresh length on frozen (thawed)lengths were then determined and these are shown in

Fig. 3. It is evident that there is very little difference in shrinkage between those capelin frozen in brine or frozen dry. The percentage shrinkage over the length range represented is approximately 3% and this factor was used to convert thawed lengths to fresh lengths.

Lengths of capelin preserved in 95% alcohol were adjusted according to Winters (MS, 1966). Larval capelin ranging from 20 to 40 mm were found to shrink 2 mm when preserved in alcohol. All larval lengths used in this paper have been adjusted accordingly.

III RESULTS

A. Otolith radius-fish length relationship of Trinity Bay capelin.

Trinity Bay was selected as the main area for the description of the relationship of the otolith radius to the total length of capelin (subsequently termed the otolith-body relationship) because it was the only area in which all ages and maturities were available for both sexes.

The increasing disparity in size existing between the sexes after their first year of life (Templeman, 1948; Pitt, 1958a) necessitated the separation of sexes in determining the otolith-body

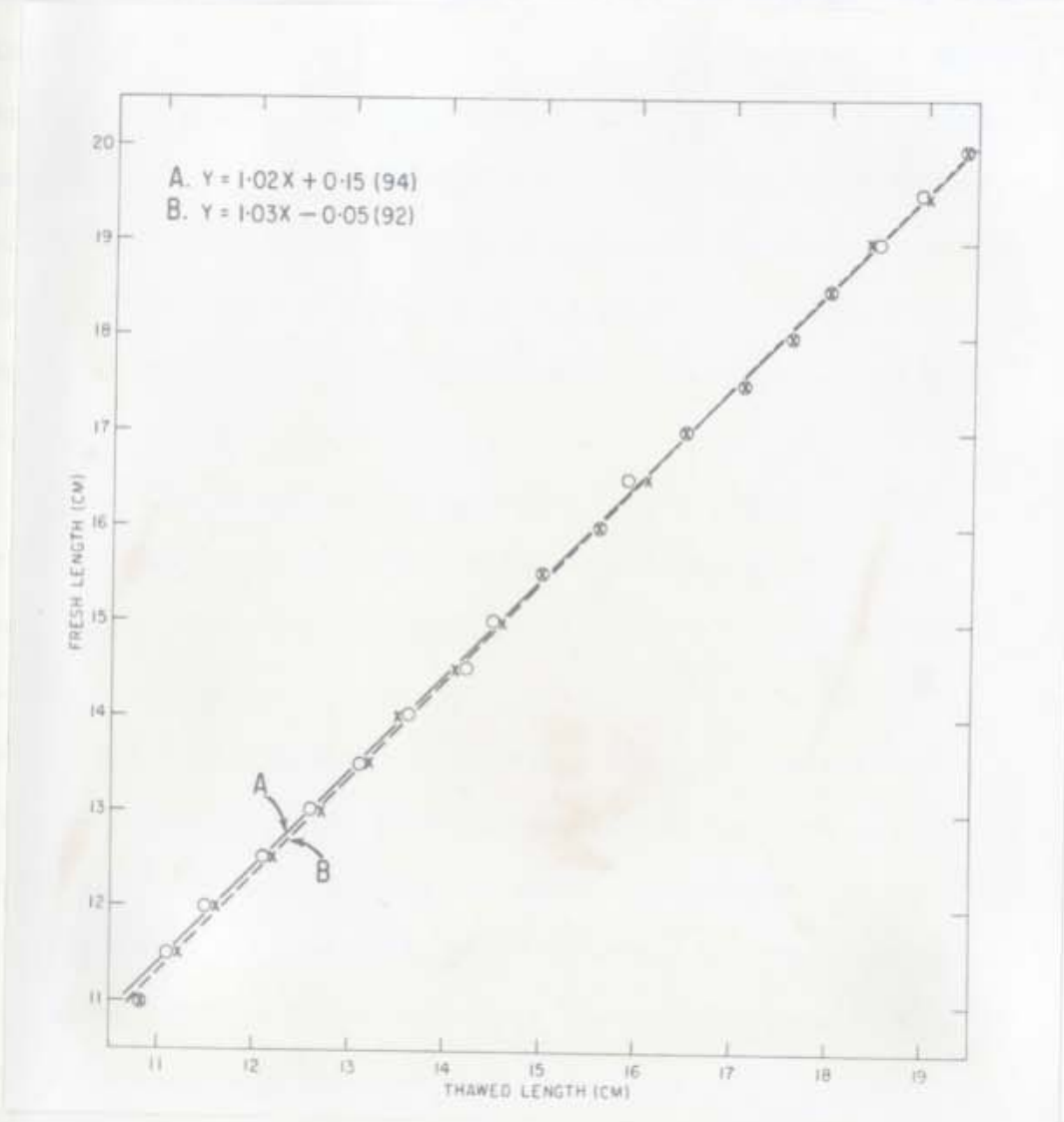

Fig. 3. Regression lines of fresh length on frozen (thawed) length of capelin frozen in brine (A) and dry (B) for a period of one week.

relationship of capelin 2 years old and older. Initially, ages and maturities were combined for each sex. The otolith radius measurements were grouped in intervals of 0.5 EPU and average body lengths in mm were plotted at the midpoint of each otolith radius interval. Approximate curves were drawn visually to represent the scatter of points for both sexes. The resulting curves (Fig. 4) indicate that the otolith-body relationship in capelin is in the form of two distinct curves with inflexion points occurring at 15 cm for males and 13.5 cm for females. This represents the approximate average size at maturity for both sexes.

Since it was apparent from the empirical curve that no straight line could fit both domes it was decided, for statistical convenience to transform the data into natural logarithms and apply log-log regressions to that portion of the curve below the inflexion point (immature capelin) and to that portion of the curve above the inflexion point (mature fish) for both sexes. However, the two domes retained their original curvature indicating that the otolith-body relationship in capelin is heterogonic in form. Consequently, it is not possible to represent the otolith-body relationship in capelin by a single mathematical formula.

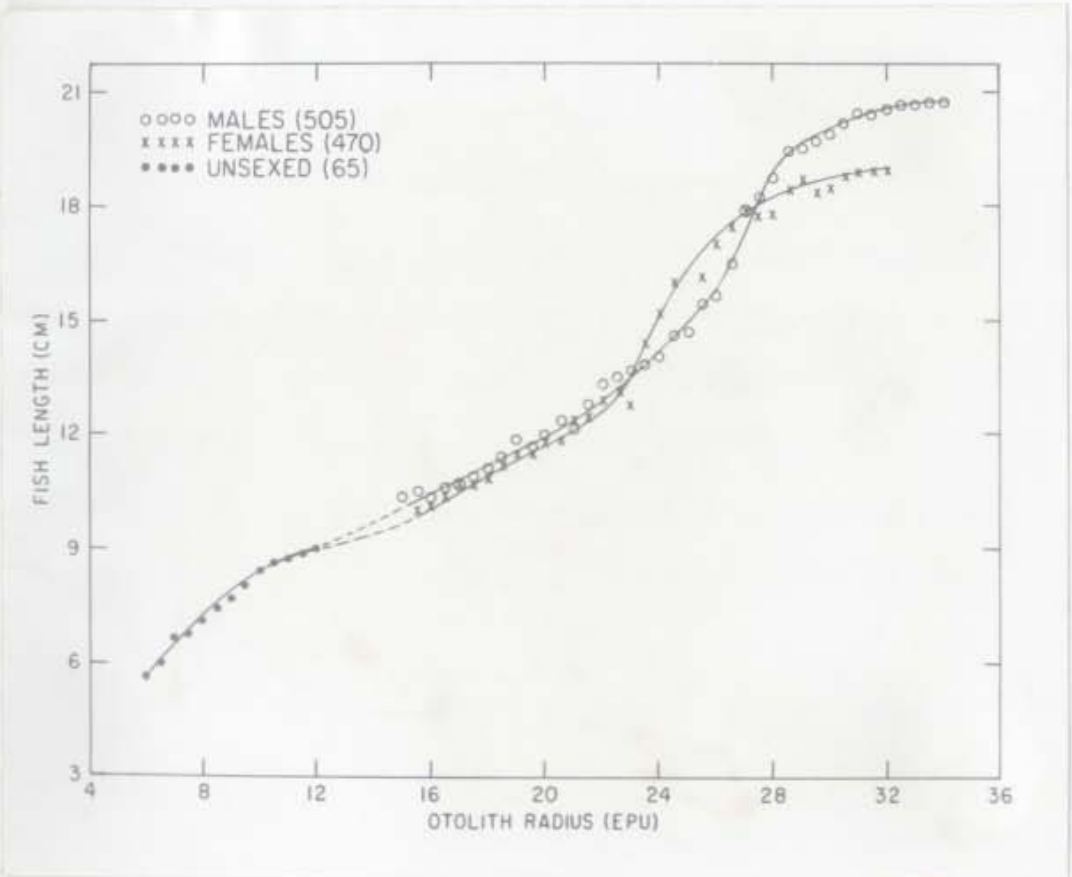

Fig. 4. Fish length plotted against otolith radius for male and female capelin in Trinity Bay. All ages and maturities are combined for each sex.

In view of this it was decided to separate the sexes into their respective ages and maturities and apply simple arithmetic and logarithmic regressions of fish length on otolith radius to each individual age. Linear correlation co-efficients were calculated for each age and Student's-T distribution was used to test the null hypothesis that there was no correlation between the two variables (i.e. C = 0). Fig. 5 gives the correlation co-efficients, T tests, regression equations, and least square lines for the various ages. It is apparent that the otolith radius-fish length relationship in capelin for each age can be adequately represented by a straight line. Log-log regression calculations gave the same results. Fig. 6 shows the gradual change in slope and intercepts with age. It may be noted from Fig. 5 and 6 that (i) mature fish have smaller otoliths than immature fish of the same size and age (ii) faster-growing fish tend to have smaller otoliths than slower-growing fish of the same size (iii) females have larger otoliths than males of the same age, size and maturity (iv) the pattern of change in slope and intercept with age is the same in mature and immature fish, i.e. the slopes gradually decrease with age while the intercepts increase. Templeman

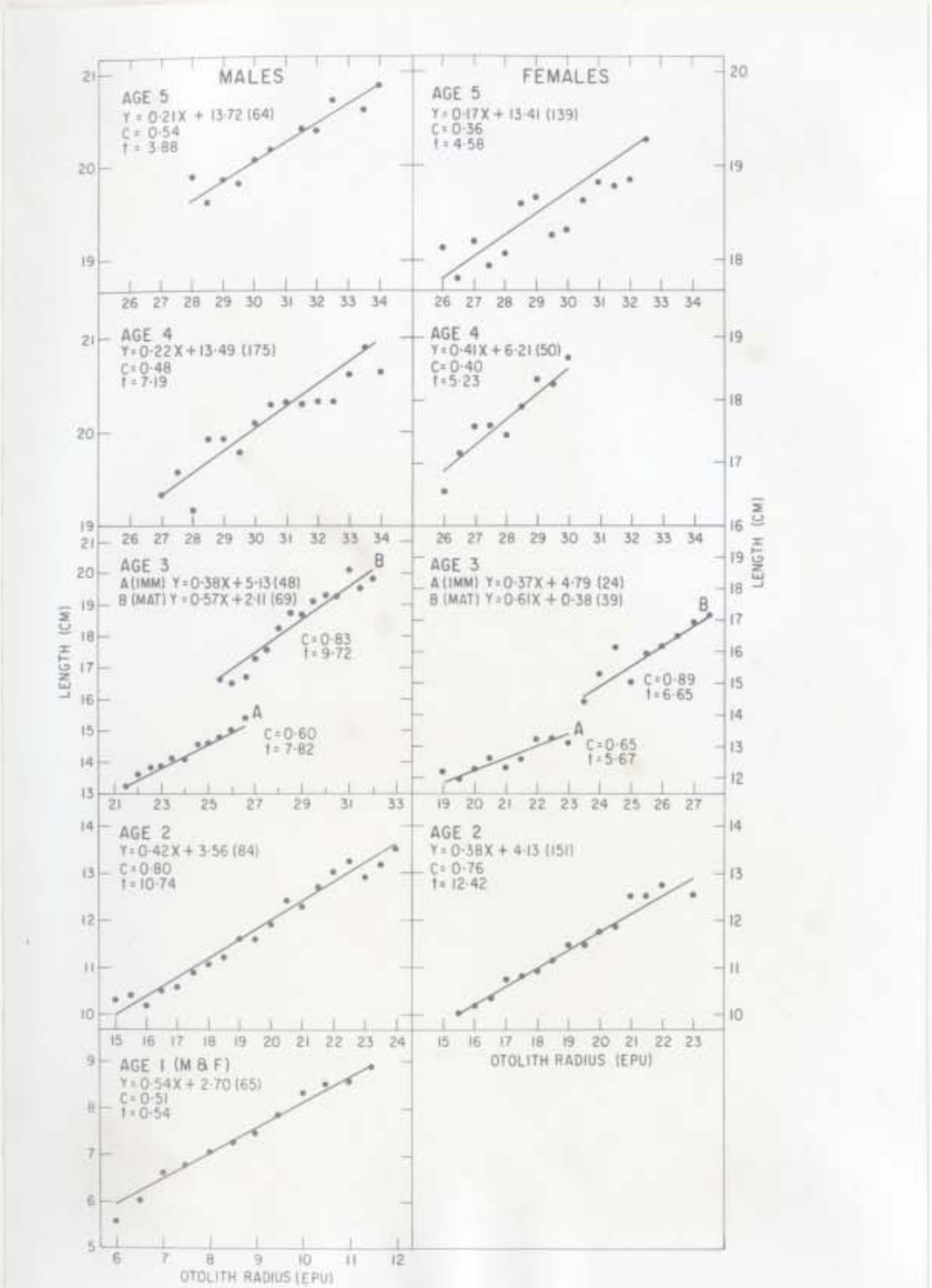

Fig. 5. Average length plotted against otolith radius for male and female capelin, ages 1-5, Trinity Bay, March 5 - June 14, 1967. C represents the linear correlation coefficient and t tests the significance of C from zero.

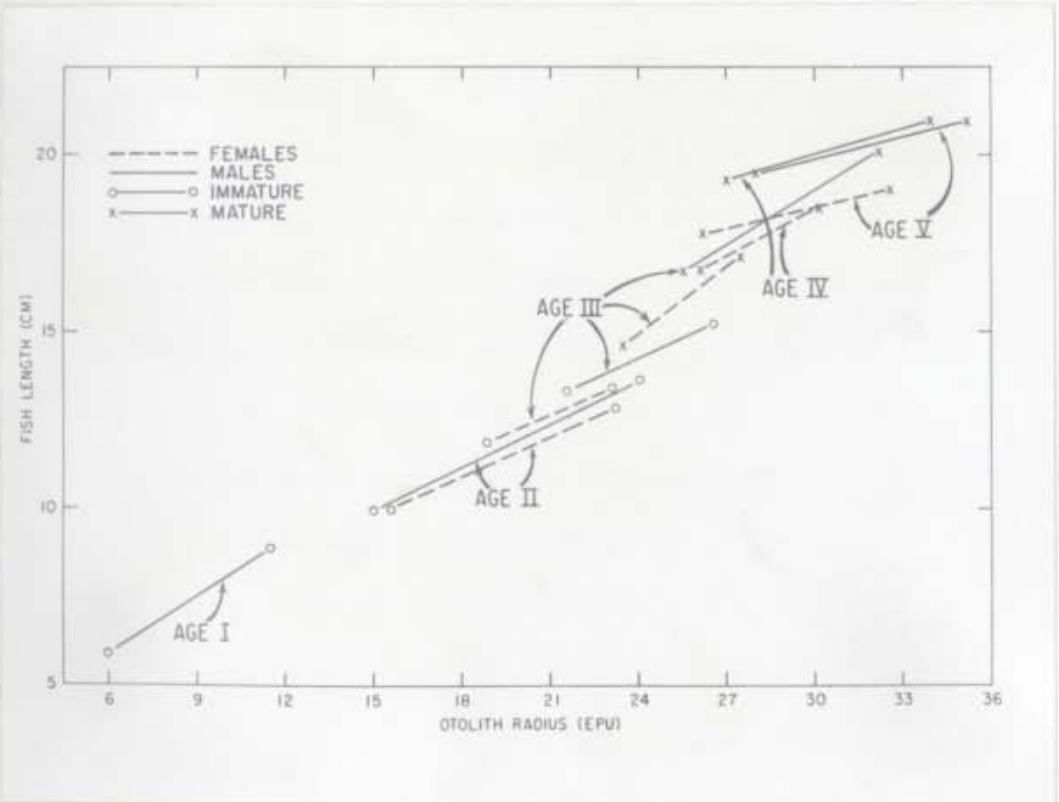

Fig. 6. Regression lines of fish length on otolith radius by age, sex, and maturity for Trinity Bay capelin.

and Squires (1956) found that haddock otoliths tended to be larger (both in terms of weight and length) in older haddock than in younger haddock of the same size. However, mature haddock were found to have heavier otoliths than immature haddock of the same size and this is in variance to the results presented above.

B. Growth of Trinity Bay capelin.

The gradual changes in slope and intercept shown in Fig. 6 necessitated the use of separate regression equations in back-calculating the lengths at each previous age for a particular age-group. Back-calculations were not made for individual fish. Instead otolith radii were first averaged for each age, sex and maturity and length estimates were back-calculated from the averaged data.

To determine the age-length relationship of capelin, average lengths were back-calculated for each age and sex and plotted against age. The resulting curves are shown in Fig. 7A. Comparison of

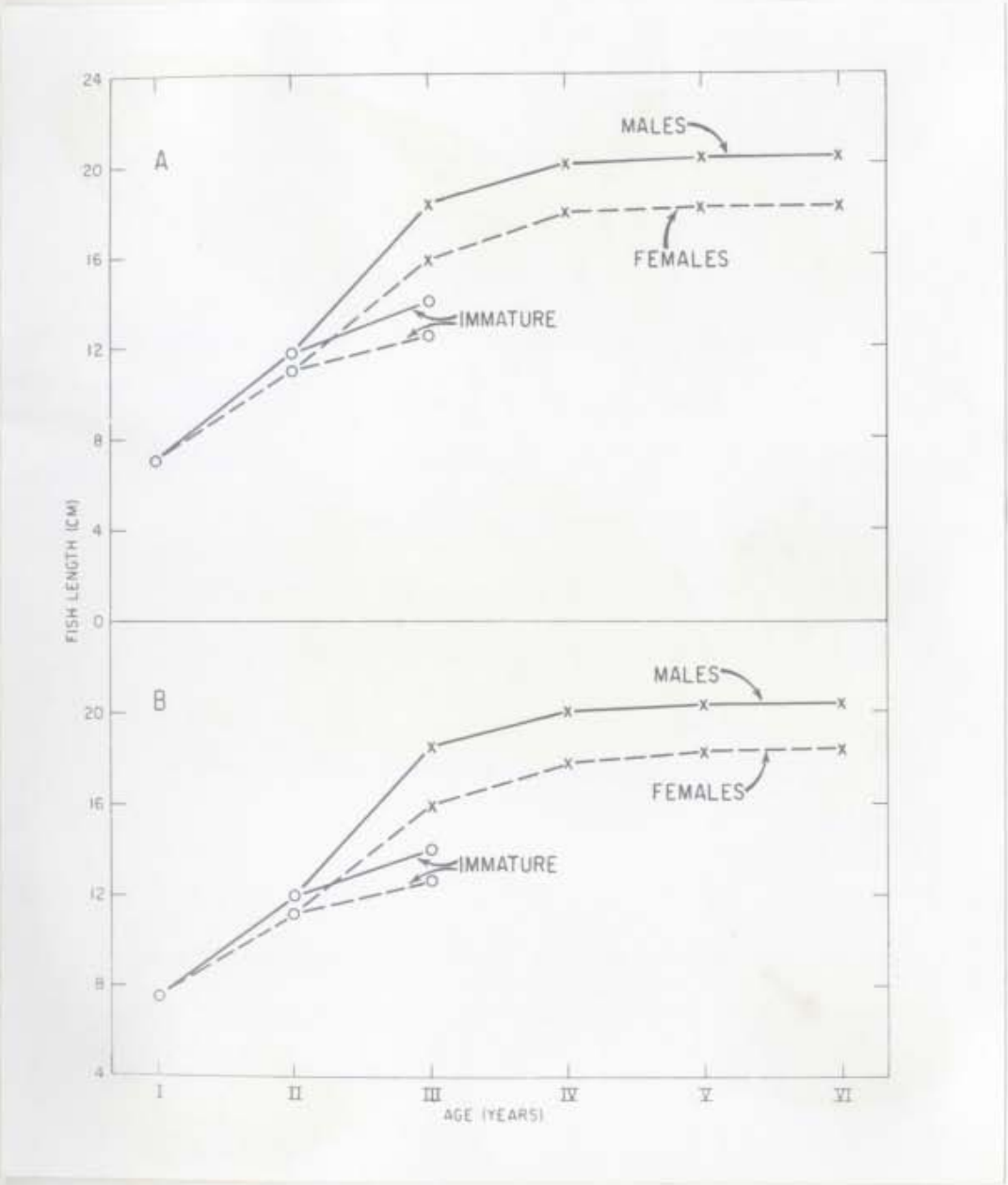

Fig. 7. Average length-at-age curves of male and female capelin, Trinity Bay, March 5 - June 14, 1967. (A) represents the back-calculated lengths and (B) represents the actual lengths.

the growth curves of male and female capelin which are mature at age 3 reveals that the greater acceleration in the growth rate of males relative to females after age 1 produces a maximum size disparity (2.5 cm) at age 3 after which the growth rates are relatively the same. However, if the average back-calculated length of immature 3-year-olds is used, the size disparity between the sexes does not reach its maximum until age 4 after which the growth rates level off at their asymptotic level. Similar results were obtained when the actual lengths at age were plotted (Fig. 7B) and the same general pattern is also evident in the length frequency curves for the various ages (Fig. 8).

Instead of average lengths it was decided to plot average otolith radii against age (Fig. 9) to determine whether or not the pattern of otolith growth was the same as the pattern of fish growth. It appears that the growth of the otolith in terms of average otolith radius is directly related to the growth of the fish in terms of average length. Consequently, instead of converting otolith radii to fish length by the regression technique, growth patterns of the fish can be accurately represented by plotting otolith radii against age. This fact is of particular

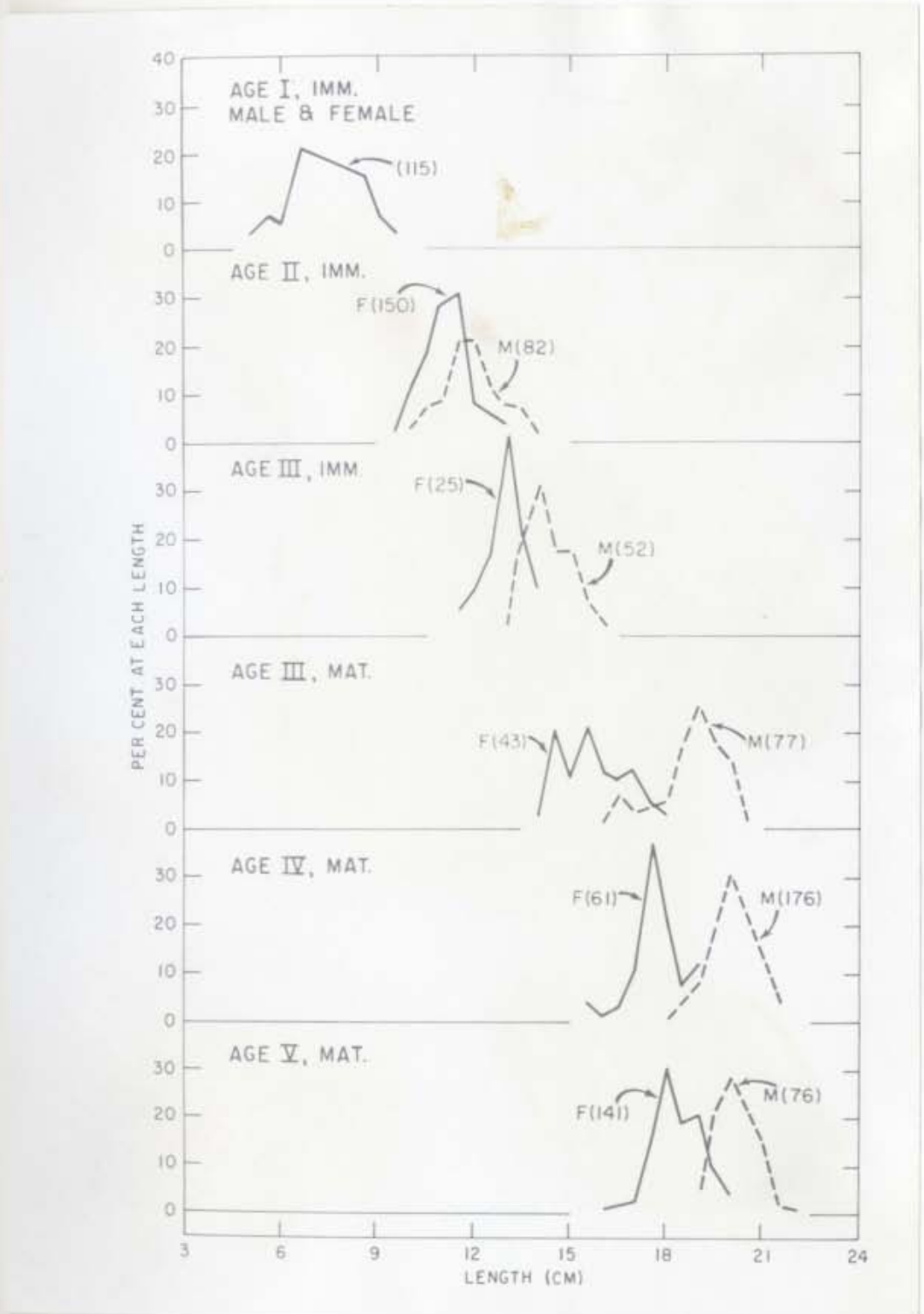

Fig. 8. Length frequency curve of male and female capelin from ages 1-5, Trinity Bay, March 5 - June 14, 1967.

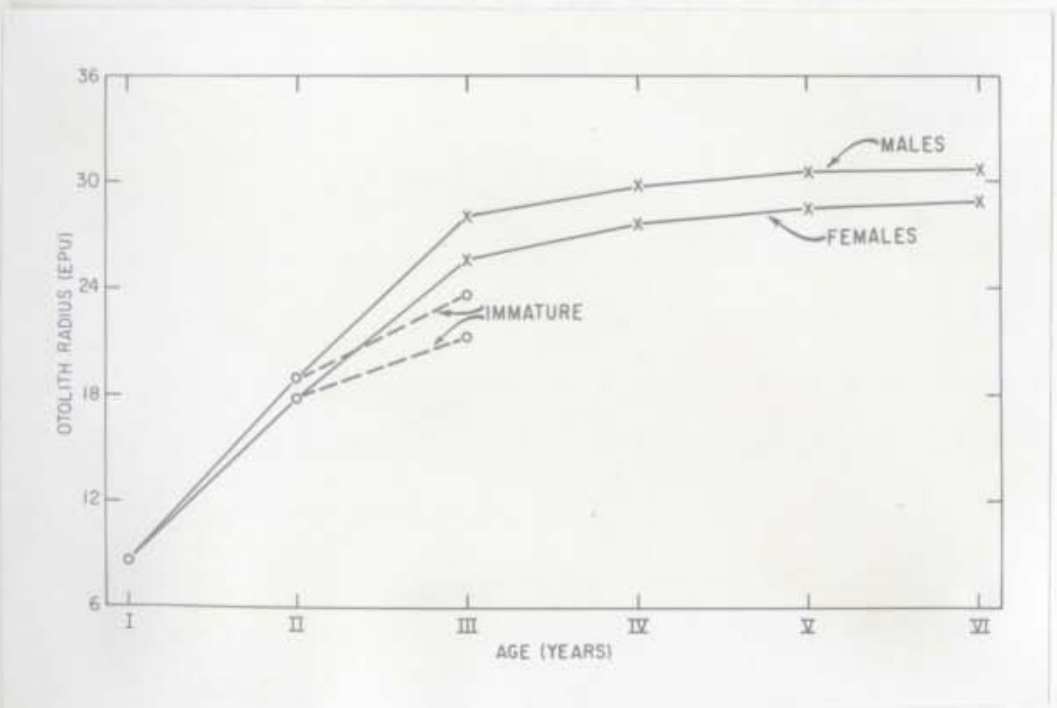

Fig. 9. Average otolith radius plotted against age for male and female capelin in Trinity Bay.

importance when the otolith-body relationship is such that separate regression equations have to be derived for each age since the absence of several age-groups, particularly the younger groups, would cause the truncation of the growth curve.

This technique will be used in a subsequent section to compare growth rates of the various areas represented in the samples.

C. Plus growth up to June in Trinity Bay capelin.

To determine the amount of plus growth in capelin for the various ages, actual lengths of capelin caught from June 4-14, 1967, in Trinity Bay were compared with their back-calculated lengths to the end of the last winter zone (Fig. 10). In general, males tend to have a slightly greater amount of plus growth than females and this is to be expected from their faster growth rate. In both sexes, with the exception of 2-year-olds, the amount of growth up to June declines from 0.7 cm in the males and 0.6 cm in the females at age 1 to zero at age 5.

The results as presented here, however, may not be truly representative of the amount of growth up to June owing to the fact that the mature fish were caught at the very beginning of the

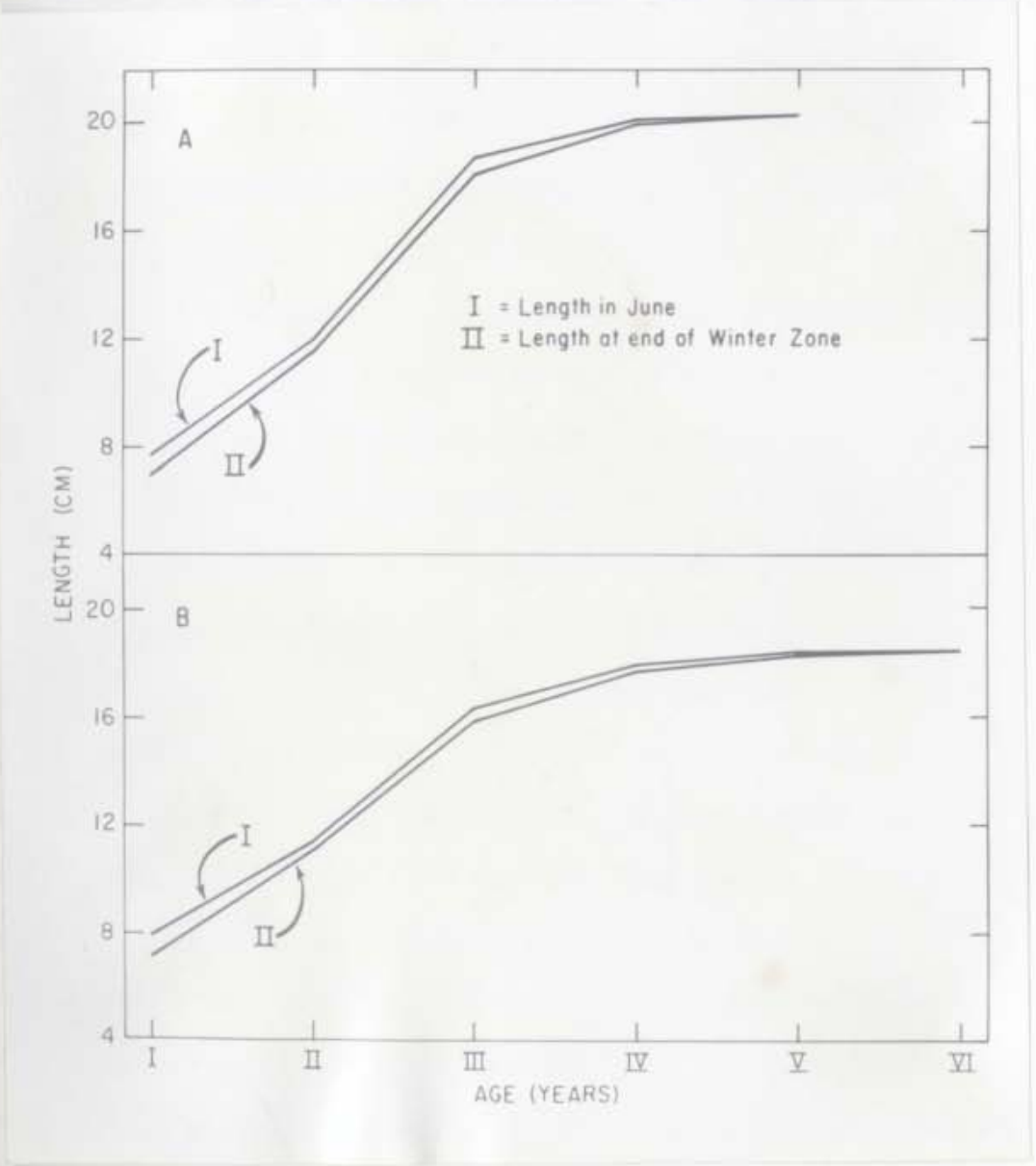

Fig. 10. Length-at-age curve of male (A) and female (B) capelin in Trinity Bay indicating the amount of plus growth up to mid-June.

spawning season and consequently represent the faster growing individuals of the year-class (Templeman, 1948; Winters, MS, 1966). This may account for the greater amount of plus growth in the mature 3-year-olds as compared to the immature 2-year-olds.

D. Inferences about age at maturity from the otolith-age relationship.

It has been demonstrated previously that the growth pattern of capelin in Trinity Bay can be adequately represented by the otolith radius-age relationship. Since the growth rate of fish in the early years of life has a profound effect on the age at first maturity (Jones, 1958), it was decided to construct curves of otolith radius plotted against age to illustrate the growth patterms of the various ages of mature capelin. The growth curves of immature 2-year-olds and of immature 3-year-olds were used as a basis for age at maturity inferences and it was assumed that these curves were representative of fish that would mature the following year, i.e. at age 3 and 4 respectively.

Before any tentative conclusion regarding age at maturity can be inferred from the growth patterns of each age, two observations about the spawning characteristics of capelin must be kept

in mind. The two observations are:

(a) Spawning mortality is greatest on the older fish, and on the larger individuals of the younger age-groups so that as a result the survivors of spawning consist mainly of younger fish and the smaller fish of any particular age-group. This can be illustrated by comparing the age and size composition of pre-spawning and post-spawning (spent) capelin. Tables IX and X give the age and size composition of pre-spawning capelin caught in June, 1967, on the eastern slope of Grand Bank and spent capelin caught in August on the Southeast Shoal. It is evident that the spent capelin are smaller at each age and contain more representatives at the younger ages than the pre-spawning capelin. Prokhorov (1960) found similar results in spent capelin from the Barents Sea. It is probable that the same situation exists in beach-spawning capelin. It is a well known fact (Templeman, 1948; Winters, MS, 1966) that the larger and older capelin are the first to spawn and remain on the spawning beaches for a prolonged period. Consequently, they would be expected to suffer a higher mortality than the smaller and younger fish which remain on the spawning beaches for only a short period and frequently spawn in

deep water near the beach after beach-spawning has ended. This deep-water spawning eliminates many of the hazards of beach-spawning.

(b) Spawning mortality is greatest in the males. Templeman (1948) referring to the beach-spawning of capelin states that "far more males than females dies from the effects of spawning" and that "it is thus probable that a much smaller percentage of males than females spawn a second time". Prokhorov (1960) found that 79% of the spent capelin moving away from their spawning grounds in the Barents Sea were females. The author surveyed the spawning grounds of capelin on the Southeast Shoal of Grand Band during early July, 1968, and found that greater than 94% of the dead spent capelin caught be bottom trawl were males, whereas nearly 98% of the surviving spent capelin were females. Also, a visual count of the dead capelin floating on the surface revealed that these were nearly 98% males. It would therefore appear certain that spawning mortality is greatest in male capelin.

Considering first the growth curves of males in terms of otolith radii at age for the ages 2 to 6 (Fig. 11A), the following

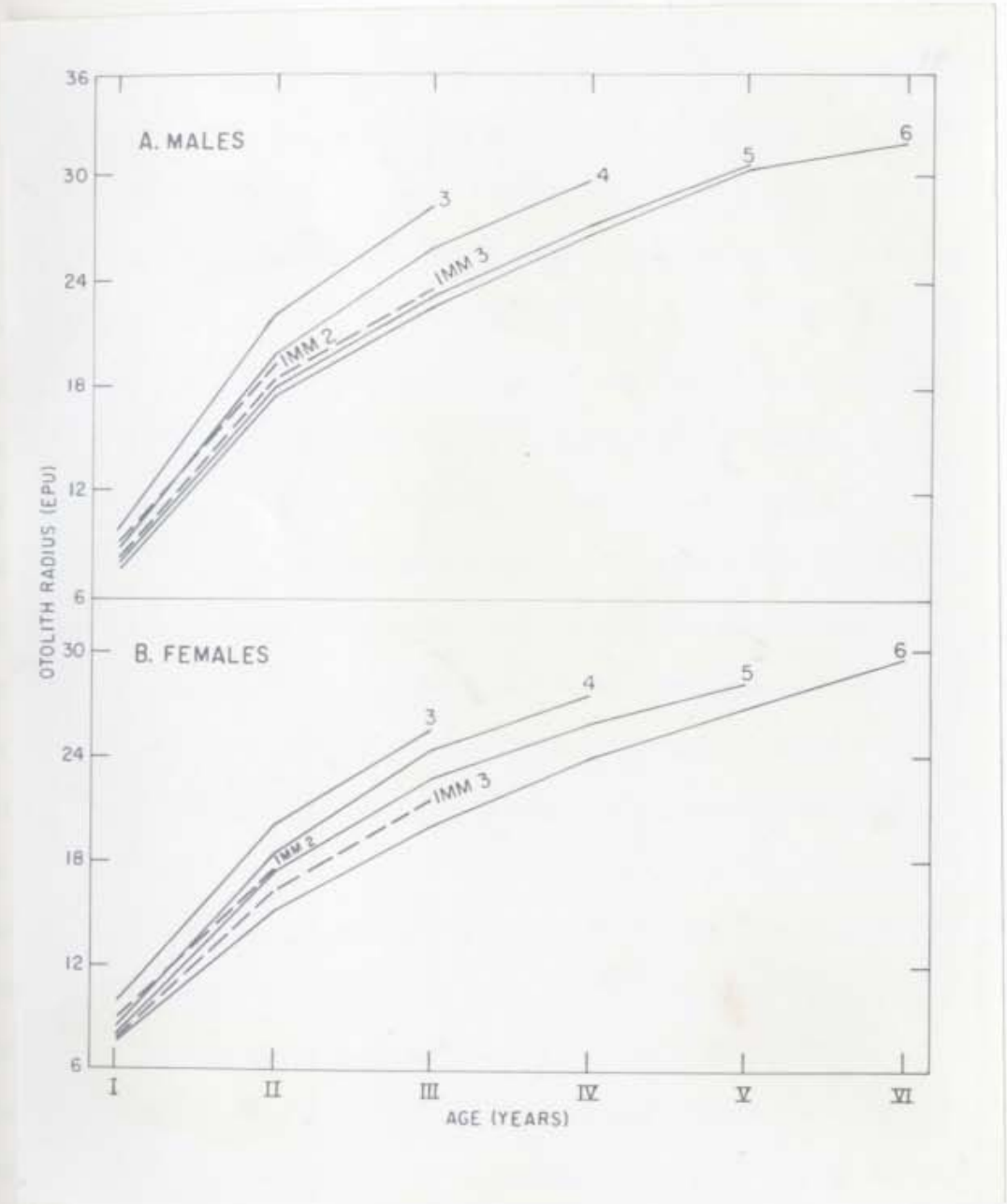

Fig. 11. Growth curves of the various age-groups of male (A) and female (B) capelin from Trinity Bay in terms of otolith-radius-at-age. Increases in otolith-radius due to plus growth are omitted.

conclusions regarding age at maturity may be made: (i) in view of observation (b) above and the lack of mature 2-year-olds in the catches in Trinity Bay, the 3-year-old mature males are mainly fish spawning for the first time. The faster growth rate of the mature 3-year-olds compared with that of the immature 2-year-olds is probably due to the fact that the mature 3-year-olds were caught at the beginning of the spawning run and hence were the fastest growing (Templeman, 1948). (ii) the close correspondence between the growth curves of the mature 4-year-olds and of the immature 2-year-olds together with the higher growth rate of the 4-year-olds relative to the immature 3-year-olds indicate that the mature 4-year-olds contain a high proportion of second spawners. The depressed growth curve of 4-year-olds compared to the mature 3-year-olds is due to (a) above and also because it includes fish which are spawning for the first time (i.e. slow growers). (iii) the close correspondence between the growth curves of mature 5-year-olds and immature 3-year-olds together with the improbability of male capelin spawning more than twice suggest that 5-year-olds contain only fish that did not mature until 4 years old. (iv) the 6-year-

olds consist of those fish which have spawned for the third time against great odds, or for some reason did not spawn until their fifth year.

Fig. 11B illustrates the otolith radius-age curves for ages 2 to 6 female capelin in Trinity Bay. Regarding the age at maturity the following inference may be made: (i) as in males, mature 3-year-old female capelin are most likely mainly first spawners with a small proportion of second spawners (ii) the much smaller proportion of immature 3-year-olds in the females than in the males together with the similarity in growth curves of mature 4-year-olds and immature 2-year-olds suggest that 4-year-old females are mainly second spawners (iii) in view of the higher growth rate of 5-year-olds relative to immature 3-year-olds together with the higher spawning survival in females, it may be inferred that 5-year-olds are mainly composed of third time spawners together with a small proportion of fish which have spawned for their first time at age 4. (iv) Six-year-olds are probably those fish which have spawned for their first time at age 4 (i.e. third spawners).

The above conclusions regarding age at first maturity for male and female capelin indicate that repeated spawnings are particularly common among the females but also among the males.

E. Lee's phenomenon and growth compensation in Trinity Bay capelin.

Based on the inferences reached above regarding age at maturity, back-calculated length-age curves were drawn for ages 3 to 6 for male and female capelin in Trinity Bay. Ages 5 and 6 male capelin were assumed to be immature at age 3 and consequently the regression equation for the immature 3-year-olds was used to back-calculate lengths at age 3 for these ages. This procedure was carried out only for 6-year-olds in female capelin. Both sexes were assumed to be immature at age 2. Fig. 12 illustrates the growth curve for the various ages. In both sexes there is an initial divergence in the growth rates of the respective age-groups followed by a distinct convergence after age 3. According to Zamakhaev (1965) this divergence and subsequent convergence of growth curves is characteristic of "Lee's phenomenon" of apparent change in growth rate with age in its typical form. Comparison of back-calculated l_1 value from ages 1-6 indicates that Lee's

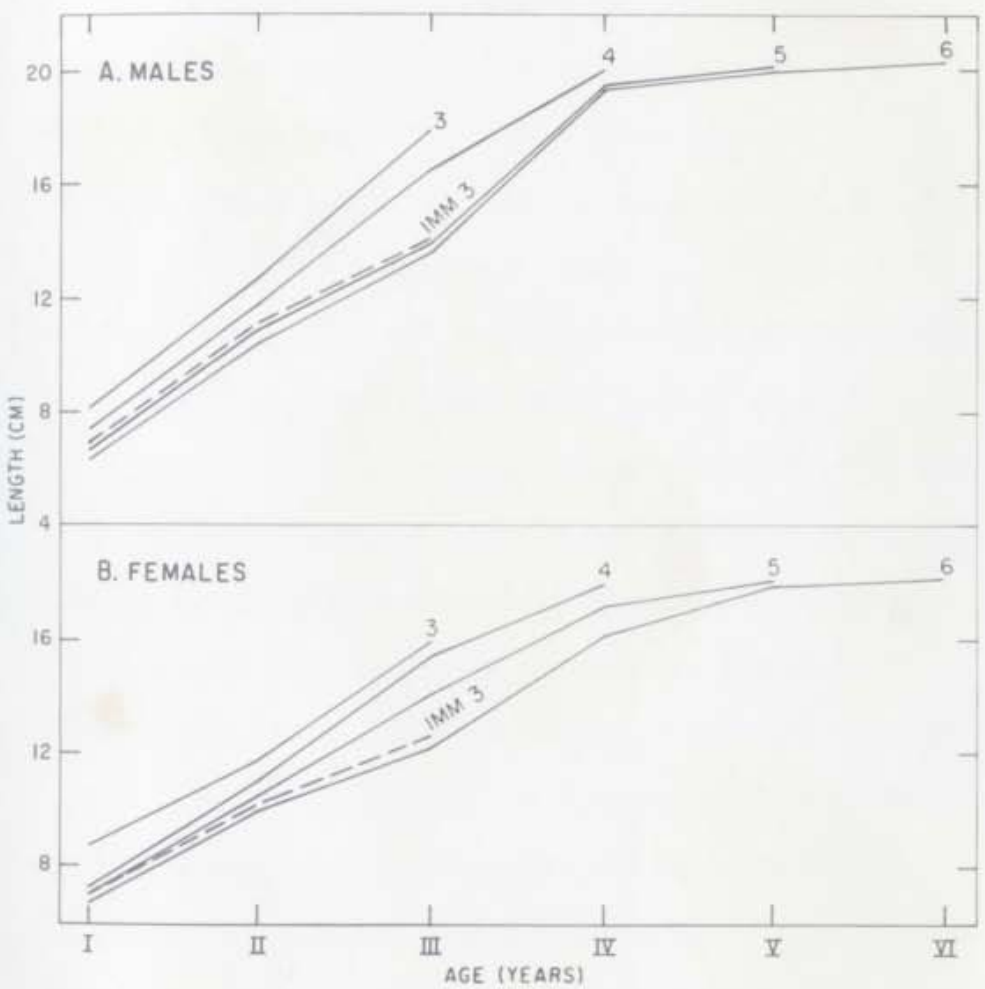

Fig. 12. Growth curves of the various age-groups of male (A) and female (B) capelin from Trinity Bay in terms of length-at-age. The lengths are back-calculated according to the assumptions on maturity given in the text and do not include plus growth.

phenomenon is clearly present in mature fish but is not well defined in the immature fish (Table II). In fact if the immature 3-year-olds (which are slow-growers) are omitted it can be demonstrated that in the earlier ages the phenomenon occurs in its reverse form i.e. increase in l_1 value with age. Lee's phenomenon cannot be explained as an artifact of the method of back-calculation because it is still apparent in the R_1 values for the various ages (Table III).

The early divergence and later convergence of the growth curves of the successive age-groups shown in Fig. 12 also represents the phenomenon of "growth compensation" between age-classes. In order to establish whether growth compensation also existed within an age-group, year-old fish of age-groups 3, 4, and 5 were divided into size groups arranged in increasing magnitude of size and then their lengths and increments in subsequent years were compared. The results are given in Tables IV and V. Growth compensation appears in both male and female capelin and tends to increase with age particularly in the males. The phenomenon is also present in the immature fish. The small difference in the final sizes attained at age 5 would suggest

that if the procedure were carried further to the 6-year-olds the initial superiority in length at the end of the first year would be completely eliminated.

In the context of the influence that growth in the first year of life has on subsequent growth, the phenomenon of growth compensation is of special interest in fish, and various explanations for its occurrence as a biological phenomenon have been given in the literature (Watkins, 1927; Runnstrøm, 1936; Smith, 1956). According to Zamakhaev (1965), Lee's phenomenon in its typical form may be regarded as the same thing as the phenomenon of growth compensation. Naturally then, in such cases they will have the same causes. In capelin, the growth compensation that exists between age-classes (Lee's phenomenon) may be explained on the basis of the assumptions on maturity given in the preceding section. First of all it is caused by the differential mortality incurred during spawning. The larger and older fish are the first to reach the spawning beaches (Templeman, 1948; Winters, MS, 1966), the first to spawn, and they remain on the spawning beach for a prolonged period during which they are thrown up on the beach or "stunned" by the pounding waves. On the other

hand the younger and smaller capelin approach the spawning beach towards the end of the spawning season and remain there for only a short time. Consequently spawning mortality is much less for these fish and as a result the survivors of spawning are mainly the younger and slower-growing individuals of an age-class. As the year-class gets older the proportion of these slower-growing fish will increase.

The second explanation for growth compensation between age-classes concerns the differing ages at first maturity. Capelin which mature earliest will suffer the depression in growth rate earliest. This depression of growth rate in maturing capelin results from the conversion of a high proportion of their food intake to genital products as is evidenced by the decline in the fat content of pre-spawning capelin (Winters, 1968). In addition, except for capelin eggs swallowed incidental to their breathing processes, spawning capelin do not feed during their spawning period (Templeman, 1948) whereas the immature capelin continue feeding (Winters, 1968). Consequently growth compensation occurs between the fast-growing, early maturing capelin and the slow-growing, late maturing capelin of the same age-group.

It is obvious that the above causes of growth compensation between age-classes do not represent the phenomenon in its true form, i.e. it results from a diminution of the proportion of fast-growers as the age-class gets older and their retardation of growth due to spawning, rather than a more rapid subsequent growth of initially slow-growing fish. In its true form growth compensation in fish is probably an inherent result of internal factors which to a considerable degree depend on the length achieved by the fish at the end of the first year of life. The fact that growth compensation exists in immature capelin (Table II) of the same age-class indicates that true growth compensation is present in the growth history of capelin.

F. Age validation of Trinity Bay capelin.

The data offered two avenues of approach regarding the validation of ages as interpreted from capelin otoliths; (i) comparison of otolith ages of young capelin with modes in the length distributions (Petersen's method) and (ii) comparison of l_1 frequency curves back-calculated from older fish with the frequency curve of 1-year-old fish.

Petersen's method which is dependent on the length increments between age-groups, is particularly applicable in capelin because they experience their fastest growth in the earlier years of their life. Examination of the length frequency distribution of young capelin captured in Trinity Bay in June, 1967, (Fig. 14) reveals three distinct, successive modes in both sexes. Otoliths of capelin in the first mode are characterized by an opaque central area outside of which is a narrow hyaline zone with a thin opaque zone at the edge (Fig. 13). These were regarded as having completed their first year of life and were beginning their second year's growth. When otoliths of fish from the second mode were examined (Fig. 13) they were found to possess two sets of alternating opaque and translucent bands with a narrow opaque deposit on the edge. These were considered to be just beginning their third year of growth. The otoliths of fish in the third mode (Fig. 13) had 3 sets of alternating opaque and translucent bands and these were considered to have completed three years of growth. The regularity in the spacing of length modes and the corresponding agreement between the number of annuli associated with each length mode suggests that the age assignations were valid.

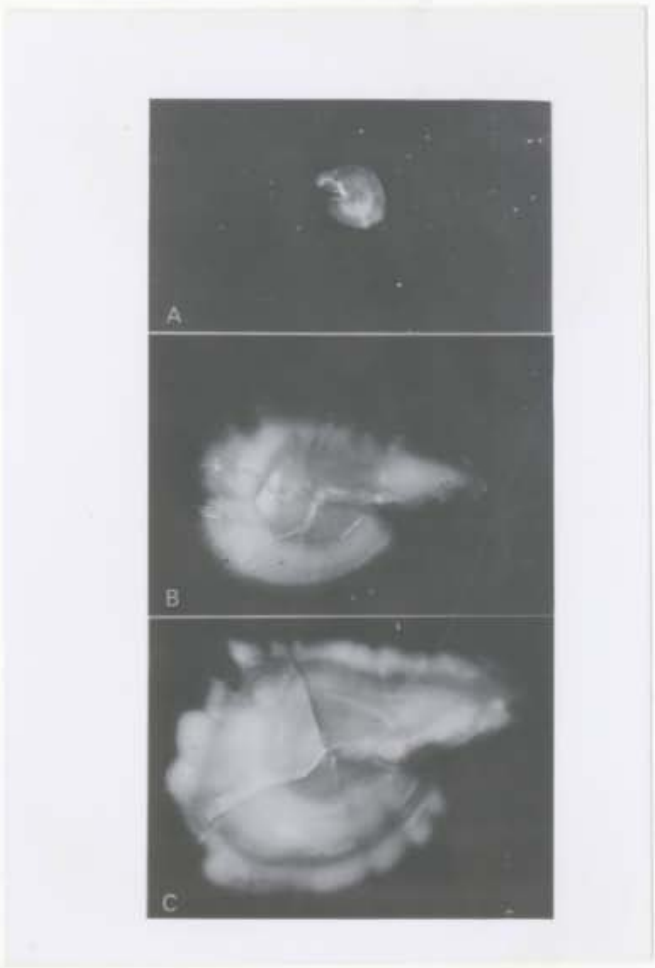

Fig. 13. Otoliths (under reflected light) X 20 of immature capelin from Trinity Bay, June 4-14, 1967. A 76 mm, 1 year; B 107 mm, female, 2 years; C 164 mm, male, 3 years.

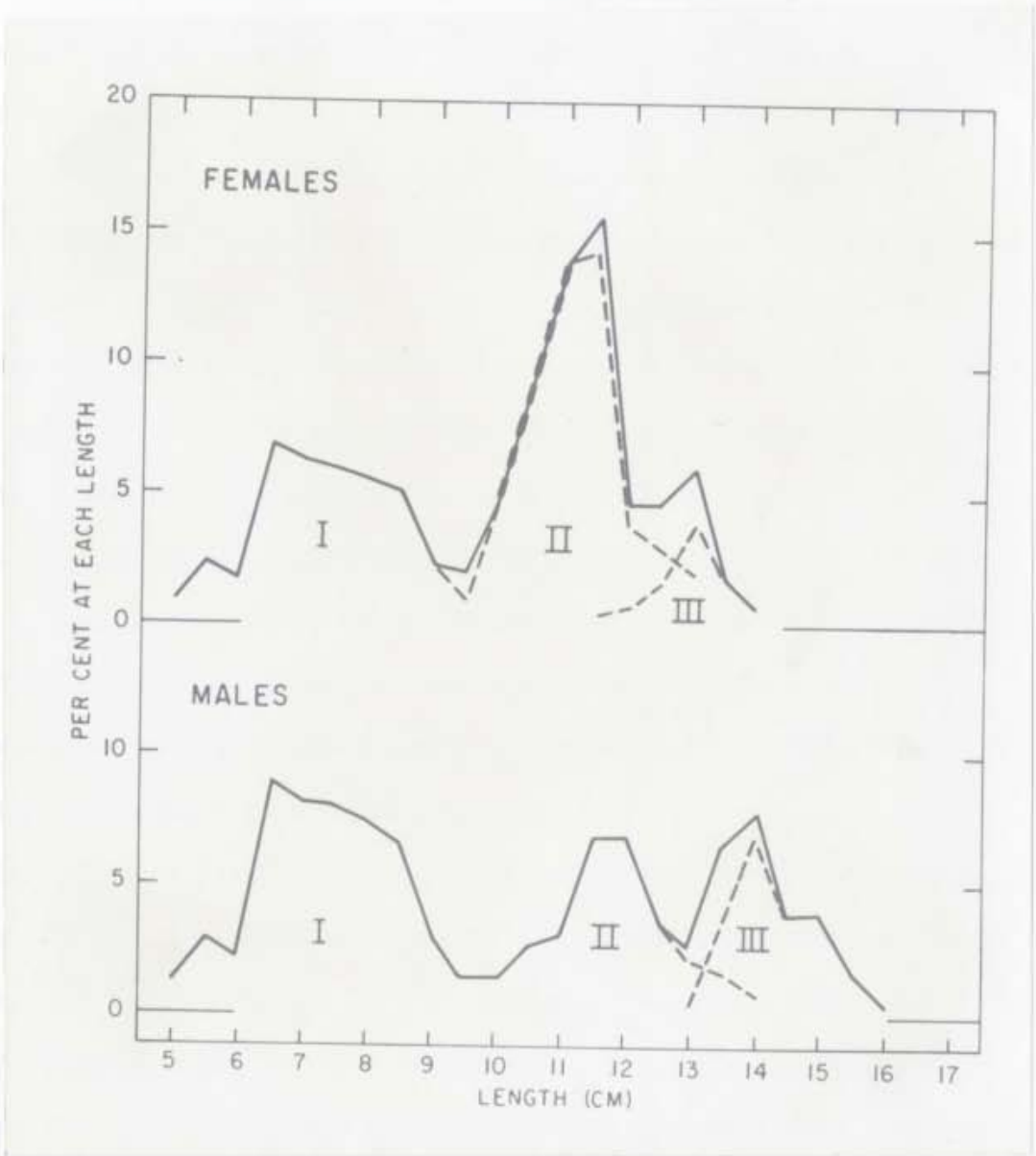

Fig. 14. Frequency distribution of young, immature capelin in Trinity Bay, March 5 - June 14, 1967. The broken line represents the length frequency distribution of the age-groups as read from the otoliths. Age-group I are unsexed but have been included in both male and female frequency curves.

The second method of age validation involving the comparison of the length distribution of 1-year-old capelin with l_1 frequency curves as back-calculated from older fish also suggests that the assigned ages were valid. Examination of the length distributions (Fig. 15) indicate that their modes all fall within a single cm interval (6.5-7.5 cm). The length ranges are also much the same with the exception that the older ages have a higher proportion of smaller fish and this is to be expected from the causes of Lee's phenomenon as previously stated.

G. Interpretation of the "larval check ring".

Near the centre of the otoliths of adult capelin inside what has been recognized as the first year of growth in Newfoundland capelin, Templeman (1948) and Pitt (1958) noted a tiny translucent area which Templeman (1968) describes as the "larval check ring". Both authors considered this central translucent area to be too small to be called the first year and hence was not included in their age readings. Recently, Templeman (1968) has suggested the possibility that this so-called larval check ring may in fact be the first year of growth in Newfoundland capelin. He bases his conclusion on a comparison of the central area of the

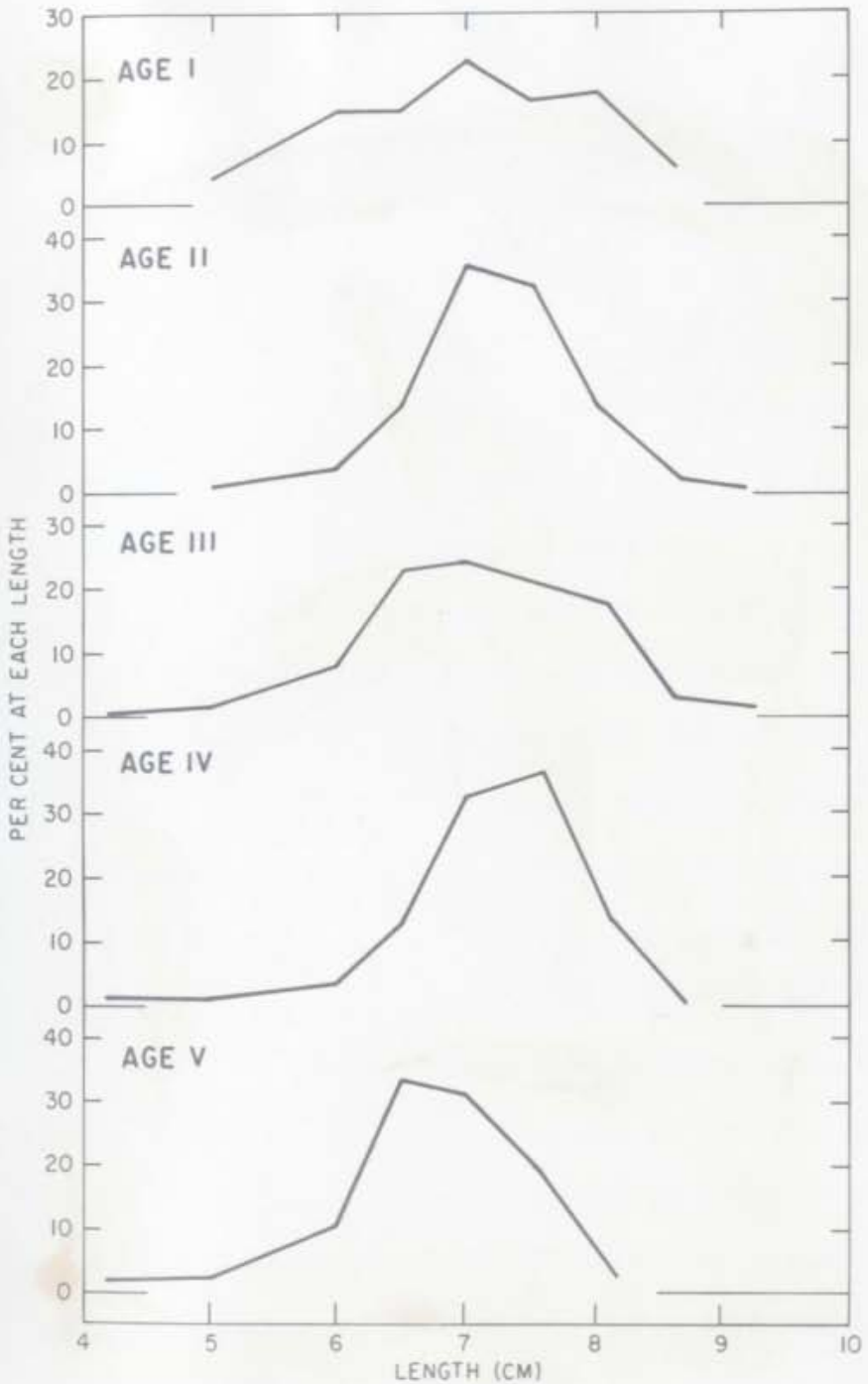

Fig. 15. L_1 frequency curves of Trinity Bay capelin as back-calculated from the age-groups shown.

otoliths of capelin from Davis Inlet, Labrador, and Godthaab, Greenland, with the larval check ring of Newfoundland capelin. It was noted that the small translucent ring in the otoliths of Davis Inlet capelin was very similar in size and appearance to the central ring of the Greenland capelin. Danish scientists (Hansen, 1948; Kanneworff, 1968) consider this small central ring to be the first year in Greenland capelin.

Recently the author obtained samples of 0-group larvae caught in October and December in Trinity Bay by the research vessel Investigator II using a 6-foot IKMT. The October larvae were caught by towing the IKMT obliquely from its initial towing depth of 45 meters (assuming a 1 in 4 ratio of net depth to warp length) to the surface in a series of 4 steps, the net being towed 5 minutes at each step. The entire bay was sampled, especially the Bellevue Beach area, where extensive beach-spawning is known to occur. Fig. 16 shows the length distribution of the October larvae. The small size and surface location of these larvae suggests that at least some of these were spawned very late in the spawning season and probably did not hatch until mid-August or later. The December larvae (4 only) were caught by oblique

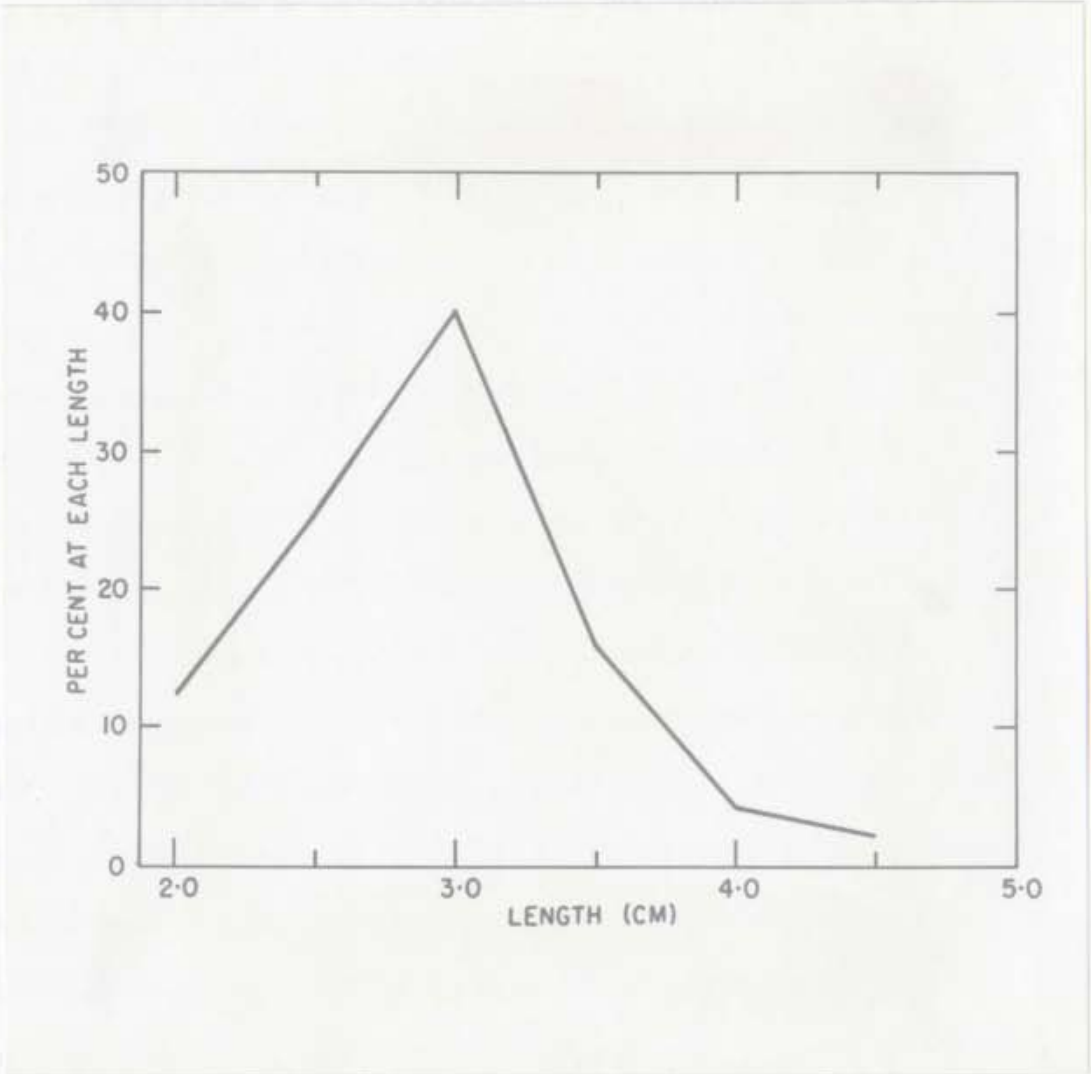

Fig. 16. Length frequency curve of larval capelin caught in Trinity Bay, October 24 - November 4, 1968.

tows from an initial towing depth of 90 meters (assuming the same net depth-warp length ratio) to the surface and ranged in length from 40 to 62 mm.

Examination of the otoliths of the October larvae revealed that all possessed a tiny central translucent area ranging from 0.4-1.0 EPU in radius. Outside of this central translucent ring, the otoliths were opaque. A curve representing the otolith-body relationship for these larval capelin was drawn visually (Fig. 17) and from this curve it was estimated that the central translucent area represented a length range of 7-17 mm. In general, otoliths of larger fish possessed a larger central translucent area. Examination of the otolith of a 62 mm larva caught in December indicated a central translucent ring 2.0 EPU in radius (Fig. 18).

The large size of this larva together with the large central translucent area of its otoliths raised some doubts as to whether it was 0+ years old or 1+ years old, i.e. hatched the previous year. Assuming that the 45 mm larvae caught in October represented the largest larvae at that time, then it would be expected that they would have been the first to hatch out. According to Templeman (1948) earliest hatching of capelin eggs on the east

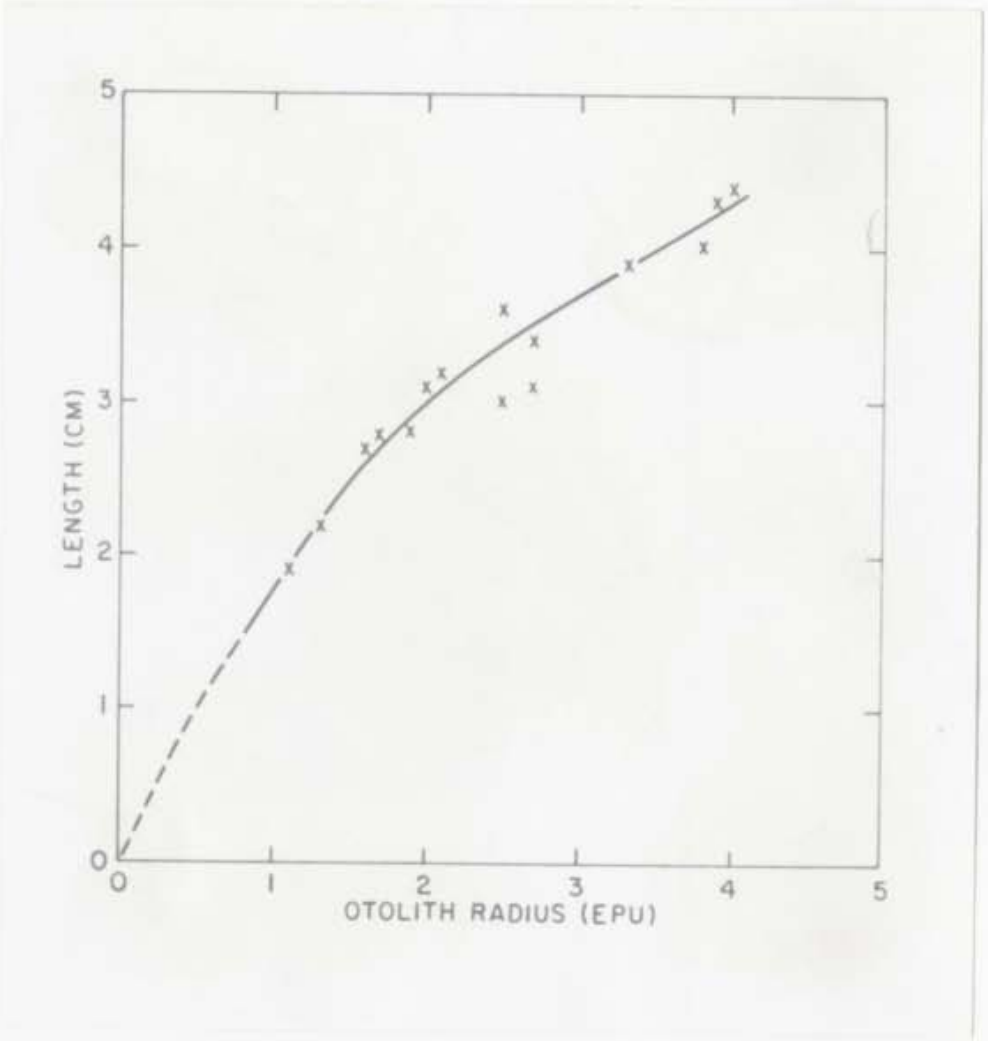

Fig. 17. Fish length plotted against otolith radius for 0-group capelin larvae, Trinity Bay, October 24 - November 4, 1968. The curve illustrated has been drawn visually.

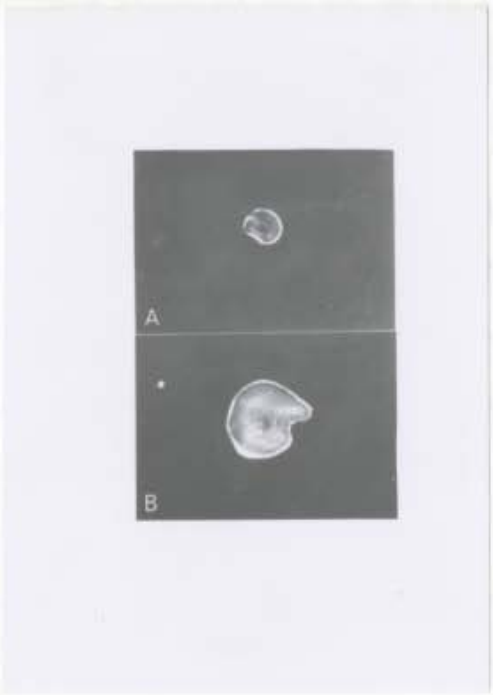

Fig. 18. Otoliths (under reflected light) X 20 of larval capelin caught in Trinity Bay, October 24 - December 16, 1968. A 38 mm 0+ years; B 62 mm 0+ years.

coast of Newfoundland occurs around mid-July so that these larvae have grown approximately 40 mm in 3 months. It is therefore not inconceivable that these 45 mm larvae in October would reach 62 mm 2 months later. In fact, as stated previously, the surface location of the October larvae suggest that they were not the largest larvae available. Thus it is quite possible that 0+ larvae 60 mm in size and larger are present in December.

The smallest 2-year-old larvae caught in Trinity Bay in early March, 1967 (Fig. 8) was 95 mm in length. In view of the cold temperature regime present in Trinity Bay after December, the 62 mm larva would not be expected to the larger than 70-75 mm by early March. The author consequently concluded that the 62 mm larva caught in December was 0+ years old and that its "larval check ring" did not represent the first year of life.

These tiny translucent rings in the centre of the otoliths of larval capelin were interpreted by the author to represent the growth of the otolith during the embryonic development of the fish. However, in capelin larvae which grow very rapidly in their first year of life the embryonic nucleus may be large enough to be misconstrued as the first year in capelin which reached a small size at the end of their first year. According to Templeman (1948) all

capelin larvae have lost their yolk sac when they reach 7 mm in length so that the larval check ring represents the growth of the fish beyond the yolk sac stage as well.

H. Interpretation of the first annual zone in Labrador capelin.

The otoliths of adult capelin from Pack's Harbour, Labrador, (Fig. 19) were much more difficult to read and interpret than those from Trinity Bay. This was due to the greater thickness of the otoliths of Pack's Harbour capelin which tended to obscure the growth features of the centre of the otoliths. In many cases, a close scrutiny of the centre of these otoliths revealed a small translucent ring or surface indentation. In view of the much larger size of the first year in otoliths of capelin from Trinity Bay, these small central rings were not included in age readings but rather were interpreted as being larval check rings. However, in July 1966, the author obtained a sample of immature capelin 79-100 mm from Davis Inlet which is approximately 2 degrees north of Pack's Harbour. The otoliths of these fish all showed clearly a small central ring outside of which there is a wide opaque ring separated from the current growth at the edge by a narrow translucent ring (Fig. 20). This small central ring was similar in size

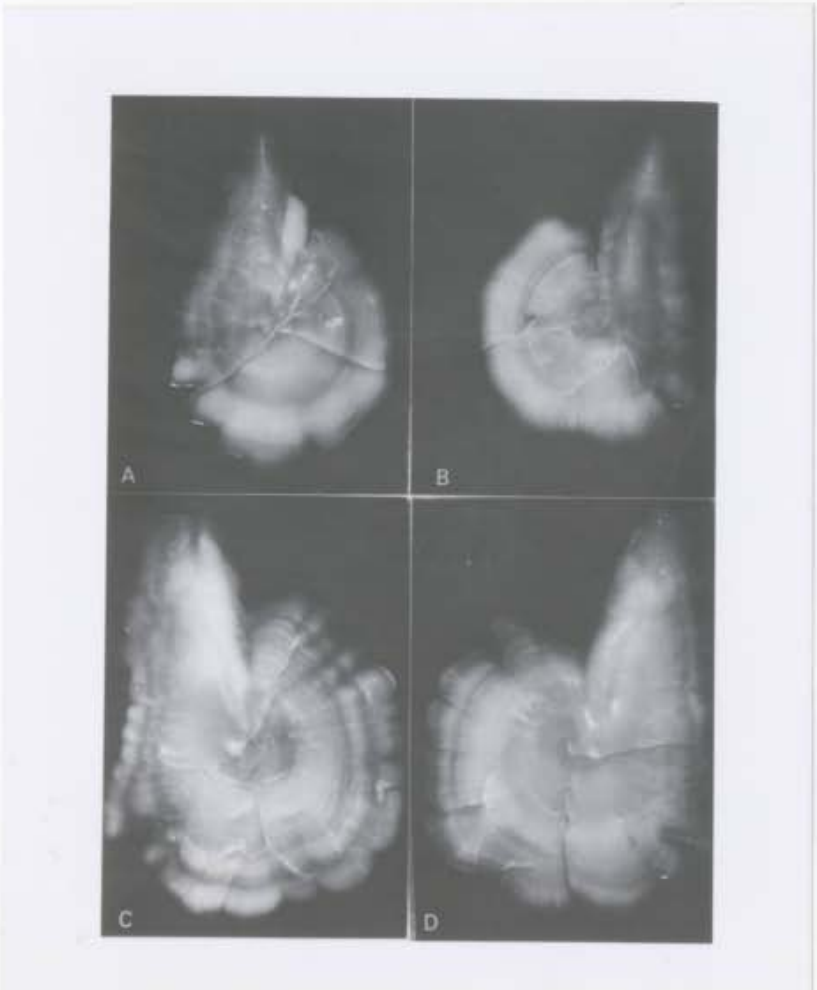

Fig. 19. Otoliths (under reflected light) X 20 of mature capelin from Pack's Harbour, Labrador, July 7, 1967. A 145 mm female, 3 years; B 147 mm female, 3 years; C 194 mm male, 4 years; D 193 mm female, 5 years.

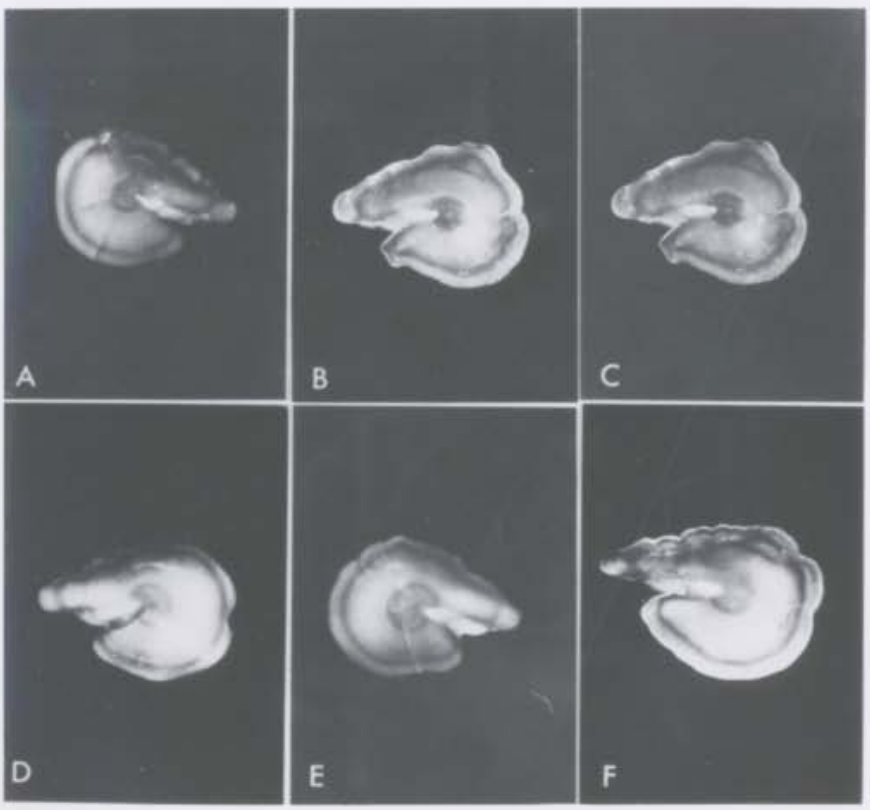

Fig. 20. Otoliths (under reflected light) X 20 of immature capelin from Davis Inlet, Labrador, July 27, 1966. A 83 mm male, 2+ years; B 83 mm male, 2+ years; C 83 mm male, 2+ years; D 84 mm male, 2+ years; E 84 mm female, 2+ years; F 92 mm male, 2+ years.

and appearance to that observed in adult capelin from Pack's Harbour. Assuming that the central ring in these otoliths from Davis Inlet does represent the first year's growth, then its small size relative to the first year in the otoliths of capelin from Trinity Bay can be explained by the northern location and subsequent later spawning (Templeman, 1948) which restricts the first year's growth. However, Templeman (1968) states that this argument appears unlikely because when these small central rings are omitted, Pack's Harbour capelin have about the same size of first year as those from the east coast of Newfoundland.

The appearance of the central ring of the Davis Inlet otoliths suggests very strongly that it does, in fact, represent the first year of growth for these fish. It is composed of an inner opaque zone outside of which is a narrow translucent zone. These zones normally represent the summer growth and winter growth respectively. Consequently these otoliths were interpreted by the author to be 2+ years old.

Recently, the author obtained a large sample of immature capelin caught by purse seine July 4, 1968 near Henley Harbour which is approximately 4 degrees of latitude south of Davis Inlet.

As in the Davis Inlet otoliths, the central ring in these otoliths (Fig. 21) is composed of an inner opaque zone outside of which is an alternating translucent zone. In addition, the radius of the central ring (3.0-9.0 EPU) of the Henley Harbour otoliths is considerably larger (Fig. 29) than the otoliths from Davis Inlet (2.0-4.0 EPU) but is somewhat smaller than the central ring (5.0-11.0 EPU) of the Trinity Bay capelin. The tiny translucent embryonic nucleus in the centre of the otoliths from Henley Harbour is similar in size (0.5-1.0 EPU) and appearance to that stated previously for Trinity Bay capelin.

Using the otolith-body relationship obtained for capelin larvae in Trinity Bay, the Davis Inlet capelin would have a l_1 ranging from 30-43 mm and those from Henley Harbour from 37-76 mm. The very narrow length range of the Davis Inlet sample suggests that it is not a random sample. These capelin were caught be a #36 otter trawl towed at a speed of 2-3 knots and the smaller fry may have escaped through the meshes. It is also possible that these may have been spawned farther north where spawning occurs later (Templeman, 1948) and were carried southward by the coastal branch of the Labrador current.

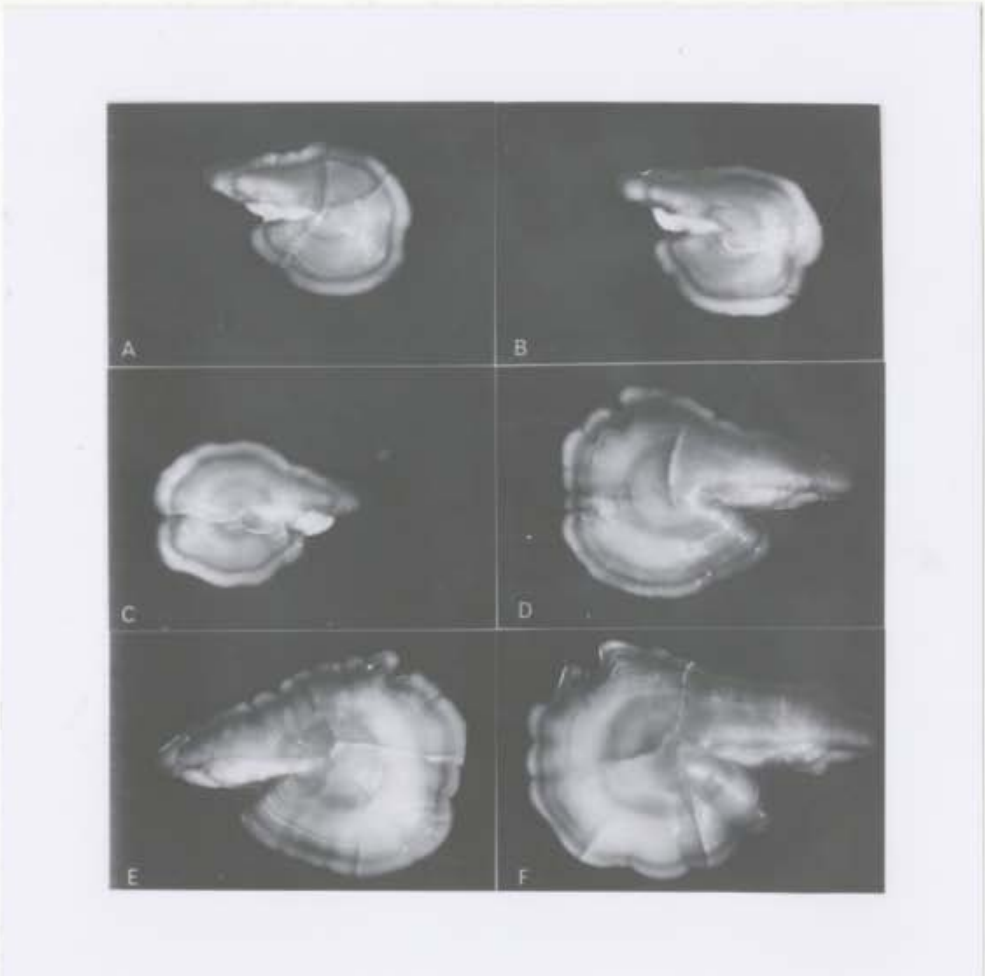

Fig. 21. Otoliths (under reflected light) X 20 of immature capelin from Henley Harbour, Labrador, July 4, 1968. A 91 mm female, 2+ years; B 101 mm female, 2+ years; C 108 mm male, 2+ years; D 133 mm male, 2+ years; E 134 mm male, 2+ years; F 156 mm male 3+ years.

Otoliths of adult capelin from Pack's Harbour (Fig. 19) had first year rings as small as those from Davis Inlet and as large as those from Henley Harbour. This intermediacy in otolith radius of Pack's Harbour capelin is consistent with its intermediate location (Fig. 1). Immature capelin caught off Cape Porcupine, which is a few miles north of Pack's Harbour, also consisted of otoliths having small and large central rings (Fig. 22).

The above material indicates that there is a decrease in l_1 values with latitude from south to north along the east coast of Labrador and Newfoundland. This is consistent with the progressively later spawning dates from south to north (Templeman, 1948).

I. Comparison of Trinity Bay capelin with other areas.

1. Otolith-body relationship.

Simple arithmetic regressions of fish length on otolith radius were applied to each of the ages available for each area. Correlation (linear) co-efficients were determined and tested for non-linearity in a manner similar to that undertaken for the Trinity Bay sample. The tests showed that in all cases the otolith-body relationship could be fitted by a straight line. The individual regression equations are given in Table VI.

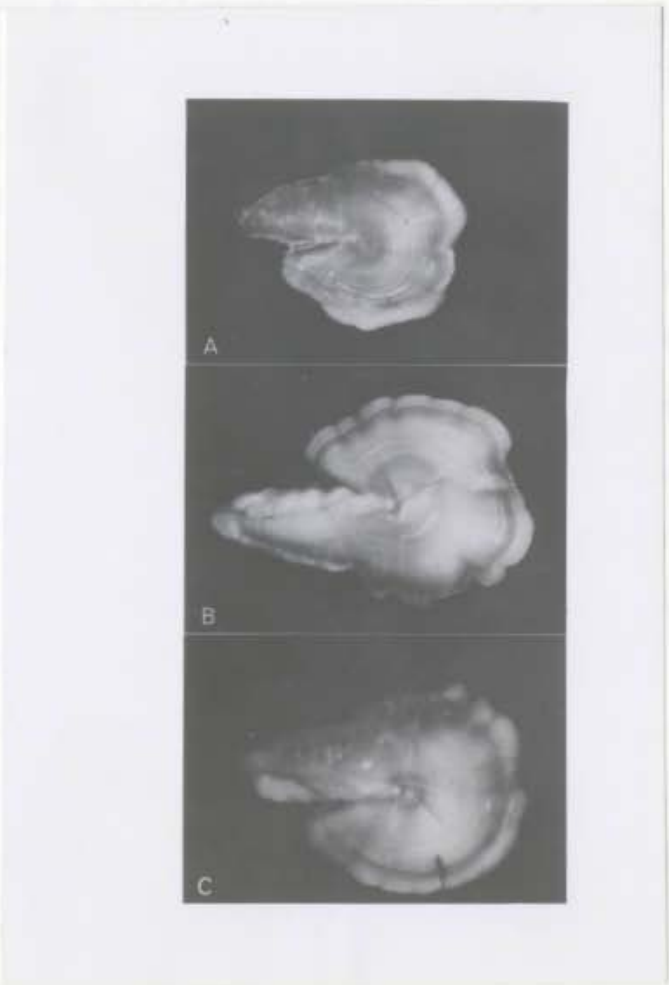

Fig. 22. Otoliths (under reflected light) X 20 of immature capelin from Cape Porcupine, Labrador, August 6, 1966. A 103 mm female, 2+ years; B 112 mm male, 2+ years; C 119 mm female, 2+ years.

In view of the already stated effects of growth rate and maturity on the otolith-body relationship of capelin it was considered that any differences that might be established by a statistical analyses of co-variance would merely reflect local variations in these factors rather than any true difference in the otolith-body relationship. Consequently the regression equations for each age and sex were not tested statistically for area differences in slope and intercepts, although it can be seen from Table VI that differences in slope and intercept do exist and that the data are better described by the separate regression lines.

A better indication of otolith-body relationships for the various areas can be obtained by comparing fish of the same sex, maturity and age range. Tables VII and VIII show the ratios of the otolith radius (in EPU's) to the total length (in cms) of capelin for fish of the same sex, age range and maturity. Thus, differences in the otolith-body relationship due to growth rate and maturity are eliminated. It can be seen that there are no consistent differences existing in the ratio of otolith-radius to fish-length between the various areas nor between the sexes. This

indicates that for fish of the same size, age, and maturity the otolith-body relationship is the same in all areas regardless of sex and that the differences apparent in the regression equations for the various areas do not reflect a real difference in the otolith-body relationship but rather are the result of local influences of growth and maturity.

2. Comparison of growth.

It has been shown previously that growth in terms of length can be accurately represented by otolith radius-age curves. Since in all areas except Trinity Bay the age compositions were restricted to only two or three age-groups, it was decided to use the otolith radius-age curves to compare the growth rates in the various areas. Age-length curves and frequency curves were used to test the validity of any differences that were apparent from the otolith radius-age curves.

Fig. 23 and 24 show the otolith radius-age curves for mature 3, 4, and 5-year-old male and female capelin from the various areas sampled. From these curves the following conclusion may be made regarding the relative growth rates of the various areas: (i) there is very little difference in the growth rates of inshore

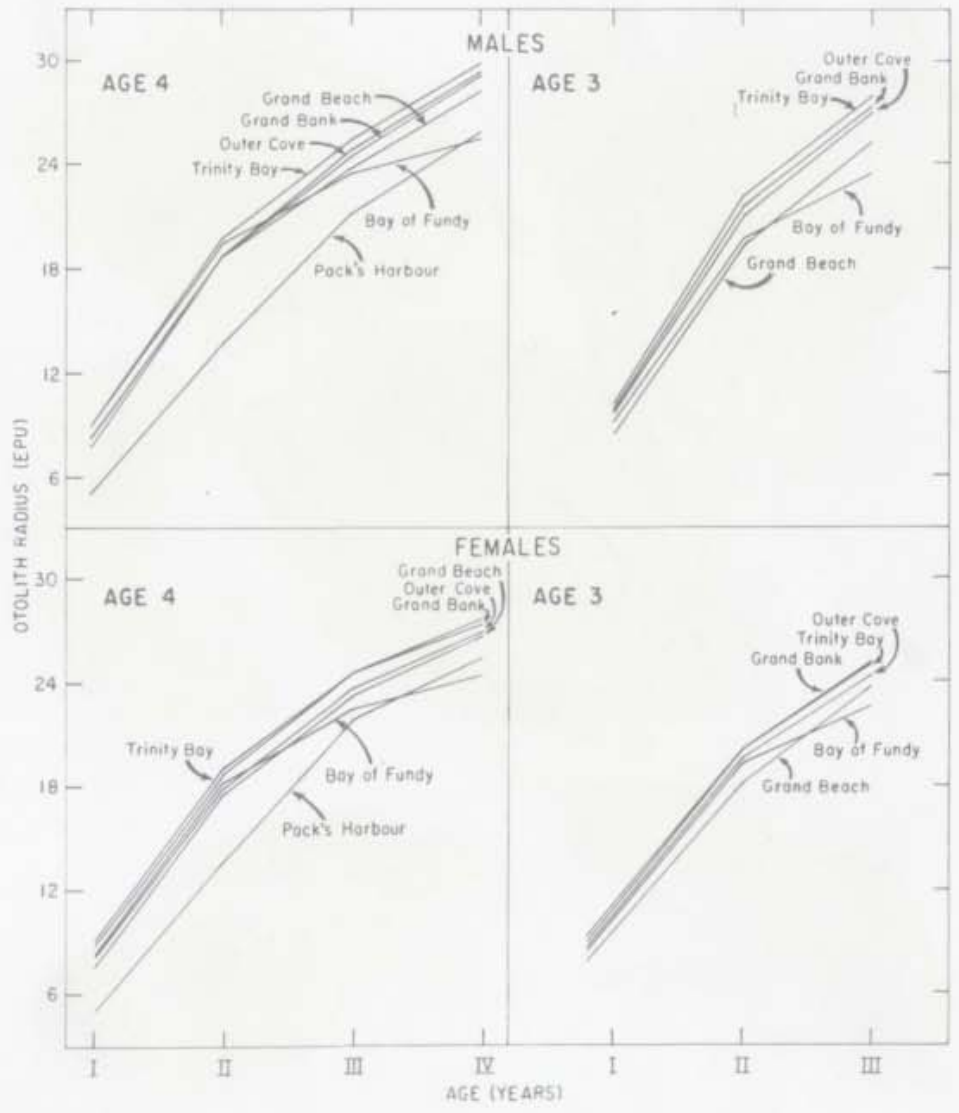

Fig. 23. Otolith radius-age curves of mature 3 and 4 year-old capelin from the various localities mentioned in the text.

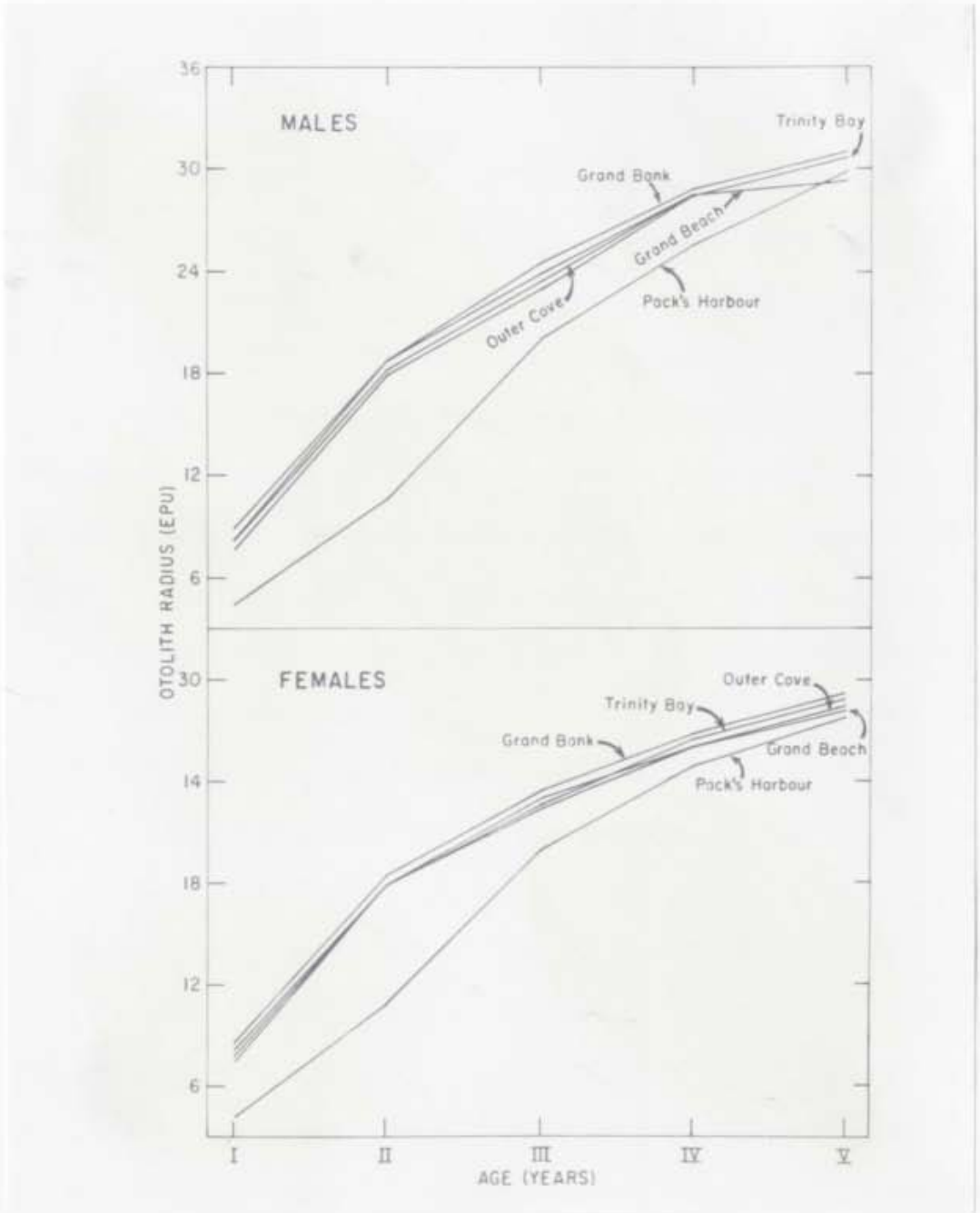

Fig. 24. Otolith radius-age curves of mature 5 year-old male and female capelin from the various localities mentioned in the text.

beach-spawning capelin from Trinity Bay and Outer Cove and the demersal spawning Grand Bank capelin, (ii) the south coast capelin represented by the Grand Beach sample appear to be slightly smaller at age than those from the east coast or Grand Bank. This, however, may merely reflect the fact that the Grand Beach sample was taken at the end of the spawning season and hence would represent the slow-growers, (iii) Bay of Fundy capelin grow rapidly the first two years of life after which the growth rate becomes greatly depressed (iv) Labrador capelin (Pack's Harbour) grow very slowly in the early years of life but growth speeds up after the second year so that by age 6 the Labrador capelin are larger than those from eastern and southern Newfoundland.

Fig. 25 shows the length as back-calculated at the end of the last translucent zone plotted against age for various areas. These growth curves support the conclusions reached above regarding the growth rates in the different areas. It is interesting to note that at age 3 female capelin from Pack's Harbour are approximately 1.8 cm smaller than those from Trinity Bay (Table IX), but at age 6 they are 0.5 cm larger. The selective effect of spawning mortality is also shown in Table IX. Spent capelin caught in August on the

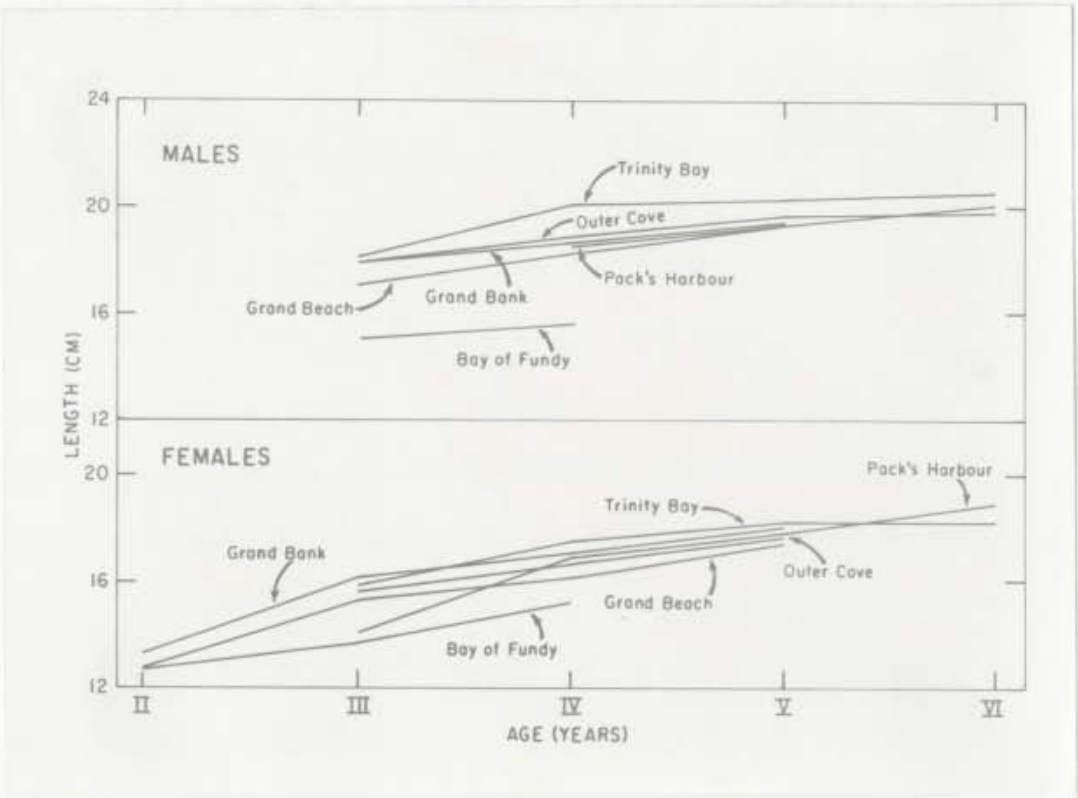

Fig. 25. Length-at-age curves of mature capelin from various localities in the Canadian area of the northwest Atlantic. Lengths are back-calculated to the end of the last winter zone.

Southeast Shoal of Grand Bank are much smaller at each age than pre-spawning capelin caught in the same area in June indicating that the faster-growing individuals of an age-group suffer a greater spawning mortality than the slow-growers.

Length frequency curves of immature 2-year-old (Fig. 26) illustrates the increase in size from Davis Inlet south to the Avalon Channel. The differences in size between the Henley Harbour and Davis Inlet samples and those from Trinity Bay and Avalon Channel are greater than shown because of the greater amount of plus growth in the Labrador capelin which were caught 1-2 months later. Length frequency curves of mature 5-year-old capelin (Fig. 27) illustrate that the size difference between the Pack's Harbour capelin and those from the east coast of Newfoundland is very small. There is thus a certain degree of growth compensation occurring between these areas. Comparison of the length distributions of mature 3 and 4-year-old capelin from the east coast of Newfoundland and Grand Bank with those from the Bay of Fundy (Fig. 28) shows that there is a distinct decrease in size in the Bay of Fundy capelin which is accentuated with increase in age.

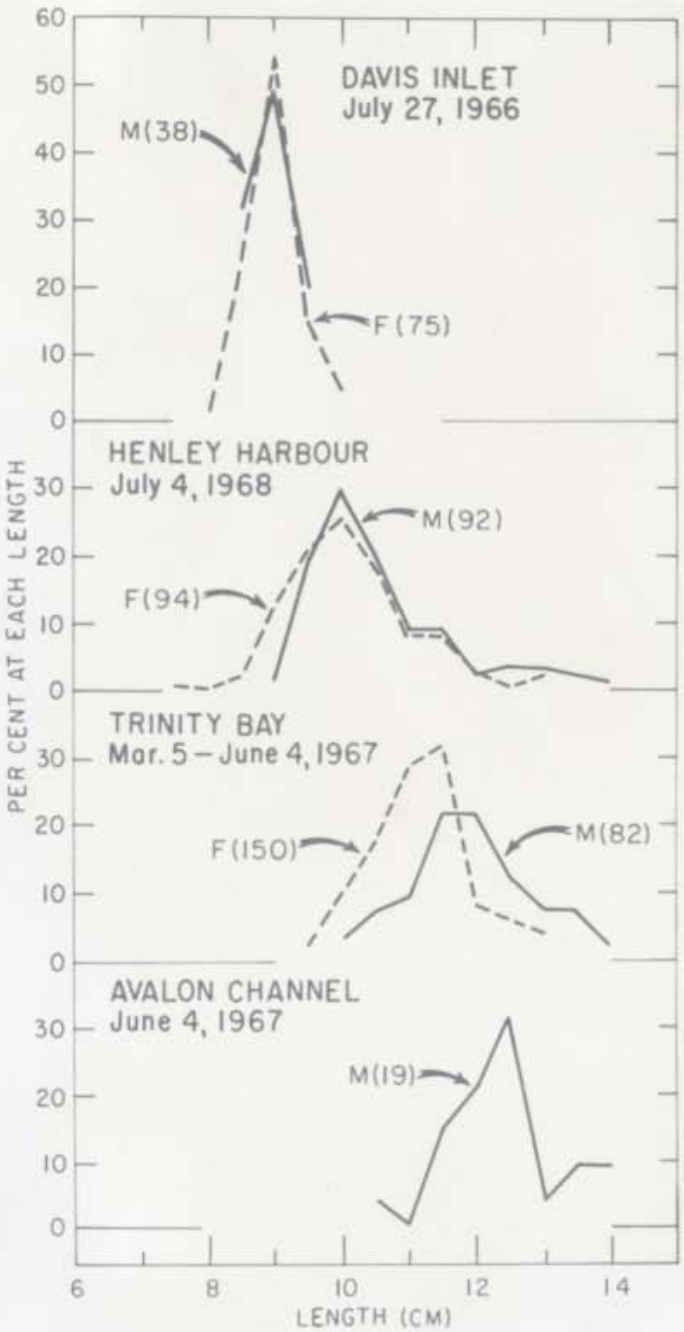

Fig. 26. Length frequency curves of immature 2 year-old capelin from various localities in the Canadian northwest Atlantic.

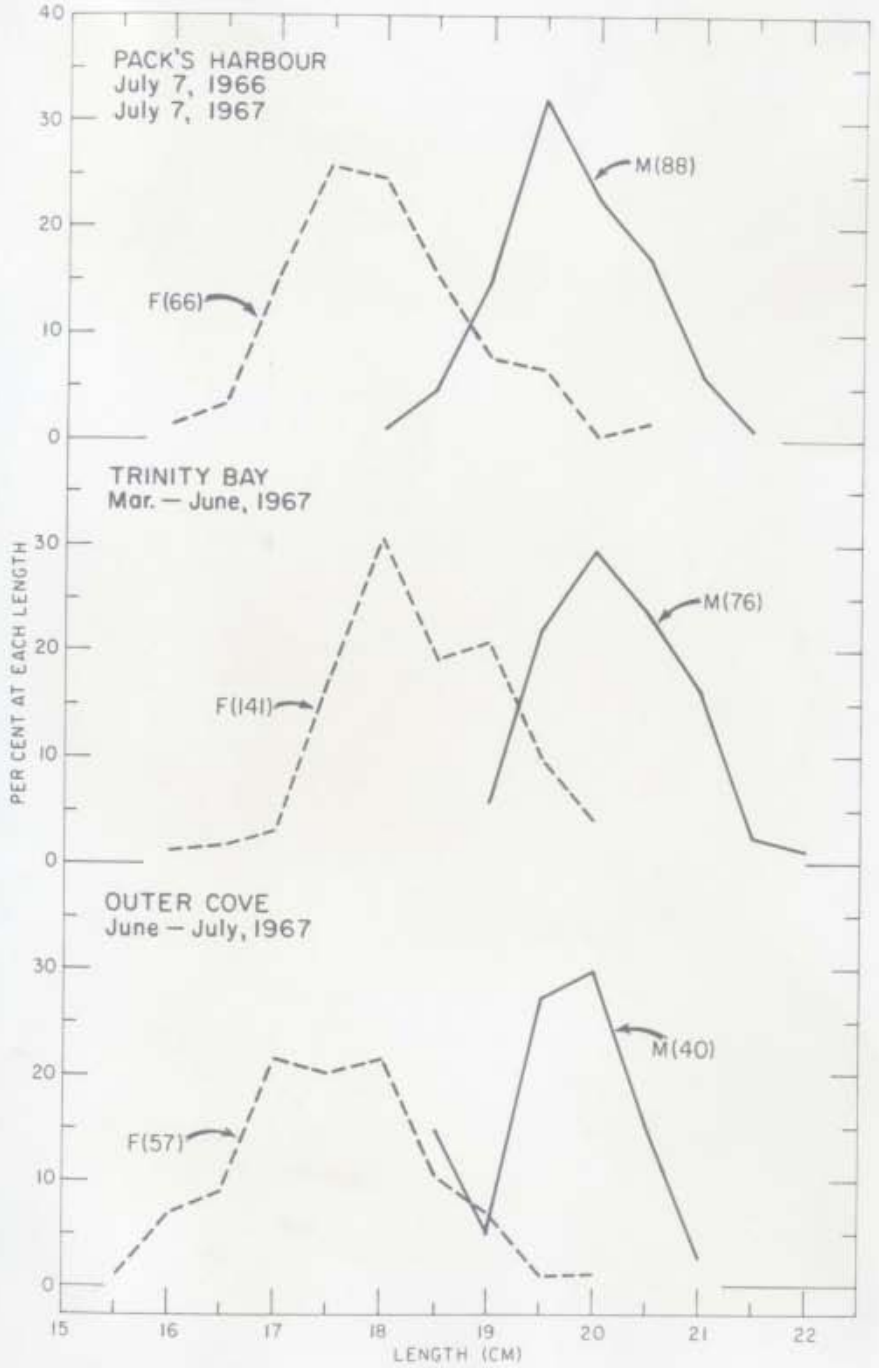

Fig. 27. Length frequency curves of mature 5 year-old capelin from various localities in the Canadian northwest Atlantic.

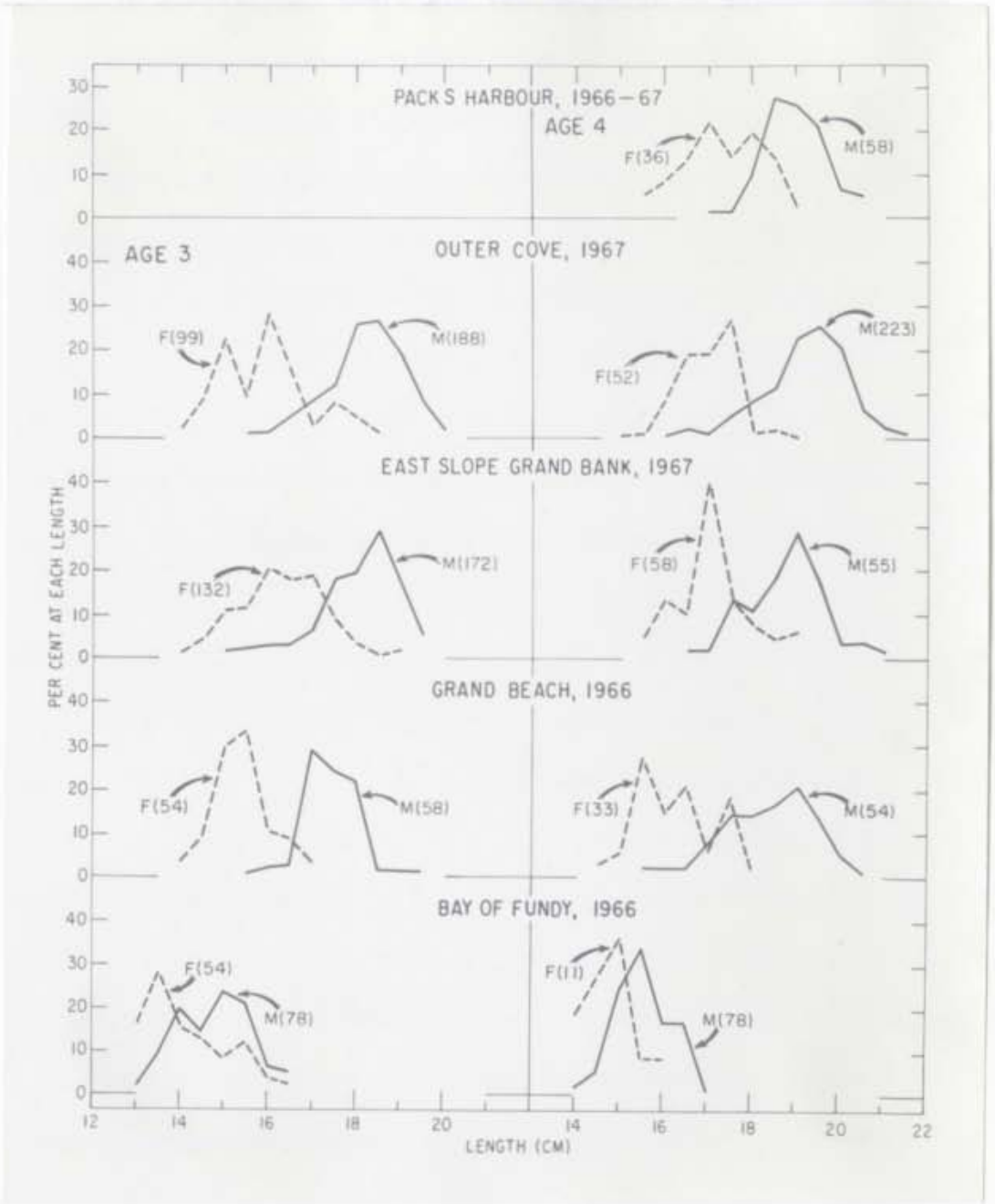

Fig. 28. Length frequency curves of mature 3 and 4 year-old capelin from various localities in the Canadian northwest Atlantic.

In conclusion, there are two patterns of growth apparent in the capelin of the Canadian northwest Atlantic. The first involves the initially slow-growing Labrador capelin whose growth rate relative to that of the east coast capelin and Grand Bank capelin accelerates with age to produce a larger maximum size. The second pattern involves the initially fast-growing Bay of Fundy capelin whose growth rate slows down with age (Fig. 25) so that there is a large size disparity in the final sizes attained by these capelin relative to the east coast of Newfoundland capelin and Grand Bank capelin.

IV DISCUSSIONS AND CONCLUSIONS

It has been shown that the growth pattern of capelin in the southern region of its range in the Canadian northwest Atlantic is a reversal of the growth trend characterizing the capelin of the northern part of its range, i.e. longevity and large maximum size in the north as opposed to a short life-span and small maximum size in the south. These patterns can be explained as the result of two contingent factors: (i) the gradual change in the spawning times from south to north (ii) the

hydrography of the areas under consideration. These two factors will be discussed separately below.

Although there are no reports on the spawning times of capelin in the Bay of Fundy, Tibbo and Humphrey (1966) report that spawning ridges were visible on male capelin from the Bay of Fundy in mid-April. Present evidence indicates that these spawning ridges develop 4-5 weeks before spawning actually begins. This would place the spawning period of these Bay of Fundy capelin as early as mid-May. This is several weeks earlier than the spawning period on the south coast of Newfoundland where mass beach-spawning usually begins the second or third week in June (Templeman, 1948). Along the east coast of Newfoundland, mass beach-spawning does not begin until the last third of June (Templeman, 1948) and the first half of July. In warm years beach-spawning in southern Labrador may begin as early as late June whereas in cold years when the ice is late leaving the coast it may be early July before spawning begins and mid-August before it ends. In northern Labrador it is usually mid-August before mass beach-spawning occurs. Pitt (1958a) reports that capelin were spawning on the Southeast Shoal of Grand Bank as late as August

during 1950 and attributes this to the effects of unusually low temperatures over the region in 1950. The author surveyed the Southeast Shoal in late July, 1967 and found that spawning had ended and that some, if not all, of the eggs were hatched as evidenced by the abundance of larvae in plankton hauls and the absence of eggs in bottom samples. Bottom temperatures in the area ranged from 0.1 to 4.8°C. According to Jeffers (MS, 1931) capelin eggs hatch out in 30 days at 5°C. This would place the spawning period of capelin on the Southeast Shoal around late June. The area was again surveyed by the author in early July, 1968 and spawning had just ended as was evidenced by the dead capelin floating on the surface. Bottom temperatures in the area were higher (0.2 to 5.7°C) in 1968. Since the spawning period of capelin is normally 2-3 weeks long, this would place the spawning period around the middle of June in 1968. There is thus considerable variation in the spawning times of capelin on the Southeast Shoal.

It is evident from the above statements that the spawning period of capelin begins progressively later from south to north along the coast of the northwest Atlantic. This difference in

spawning times may be as great as three months between the Bay of Fundy and northern Labrador. It follows from this that a truncation in the length of the growing period in the first year of growth would gradually occur from south to north. This can be determined by measuring the size (radius) of the first ring in the otoliths of capelin from the various localities. This has been done in Fig. 29 and 30. The Bay of Fundy capelin have a slightly larger first year ring than those from the Newfoundland area. There is very little difference in the size of the first year annulus in the samples from the Newfoundland area and Grand Bank. However, there is a very distinct decrease in the size of the first annulus in the Henley Harbour, Pack's Harbour and Davis Inlet compared to the Newfoundland samples and the Bay of Fundy samples. This is to be expected from the much later spawning times in Labrador.

The Bay of Fundy capelin have thus a considerable size advantage over the Labrador capelin at the end of the first year of growth. Using the otolith-body relationship for young capelin fry in Trinity Bay, the Bay of Fundy capelin would be 40-76 mm in length at the end of their first year as compared to 30-43 mm

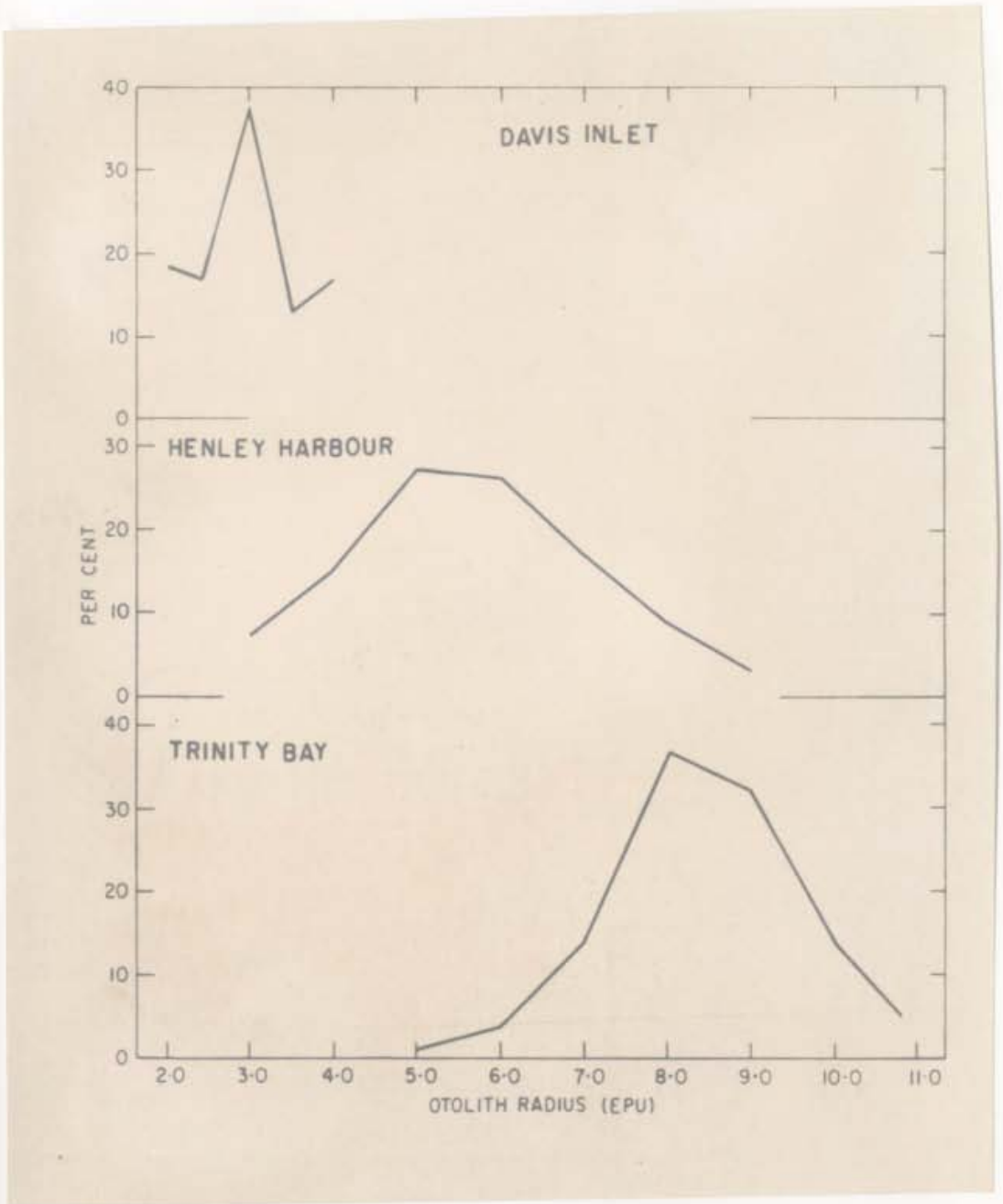

Fig. 29. R_1 (radius of the first year) frequency curves of immature 2 year-old capelin from the various localities mentioned in the text.

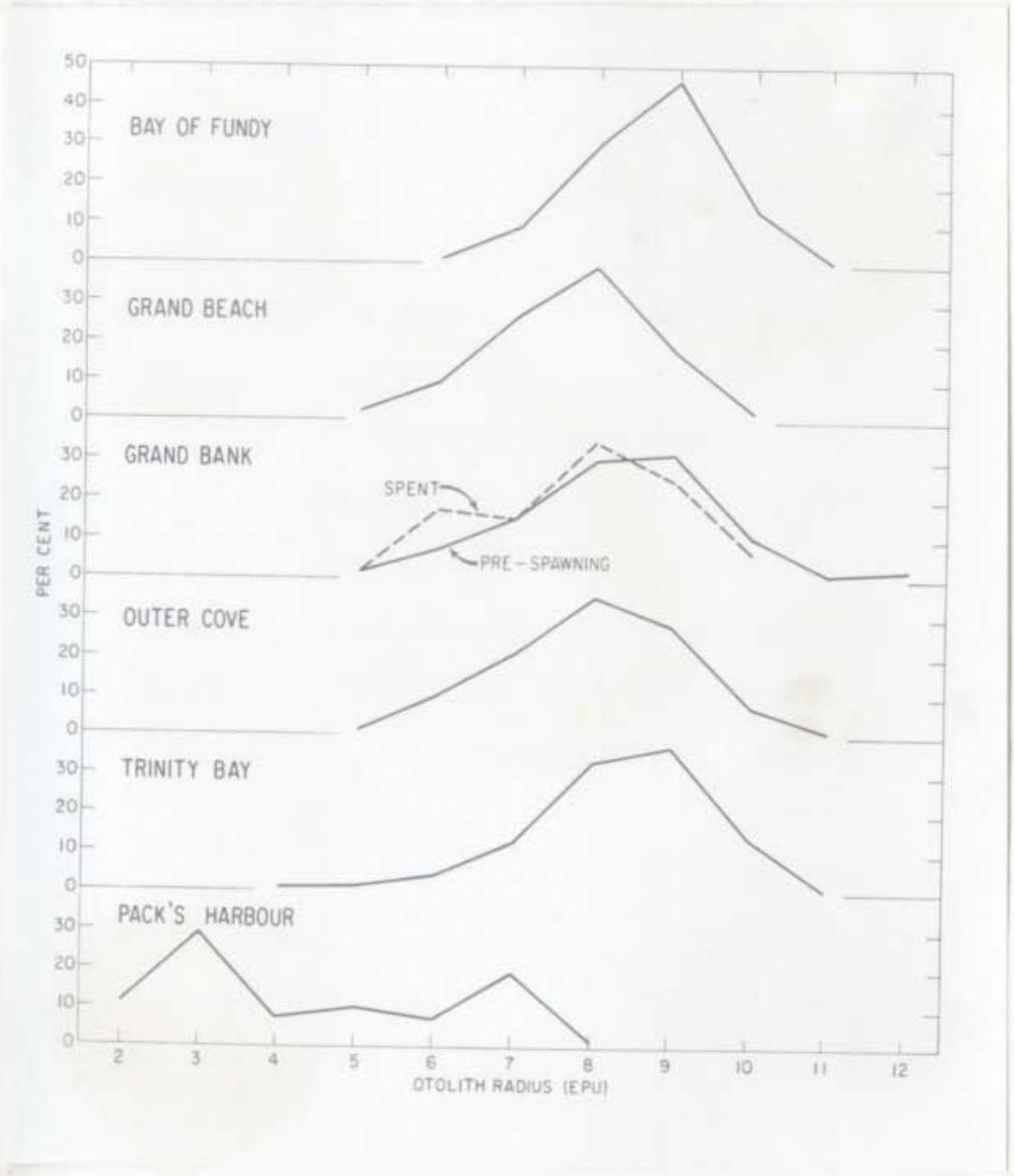

Fig. 30. R_1 frequency curves as measured from the otoliths of mature 4 year-old capelin from the various localities mentioned in the text..

for those from Davis Inlet. In the context of the influence of the first year's growth on subsequent growth Kiselevich (1922) came to the conclusion that "the first year of growth always without exception has a dominant and controlling influence on further growth. Individuals which have grown more rapidly during their first year of life maintain their superiority over their contemporaries all their lives and reach sexual maturity one or two years earlier than they do". It has been demonstrated in Trinity Bay capelin that the larger individuals reach sexual maturity first. However, the superiority in length achieved at the end of the first year by the faster growing individuals is not maintained throughout the life-span but is eliminated by growth compensation. Examination of the age composition of mature fish (Table X) from the areas under consideration, indicates that the Bay of Fundy capelin, because of their size advantage at the end of the first year of growth, mature at age 2 whereas those from Pack's Harbour, Labrador, are usually 4 years old before maturity occurs. Capelin from the south and east coasts of Newfoundland and Grand Bank appear to be intermediate in age composition.

We have seen that the initial difference in growth patterns between the north and south of the capelin's range in the northwest Atlantic is a result of a progressive change in the spawning times in each locality. The reason for this progressively later spawning times from south to north is readily apparent from the hydrography of the area under consideration. The Labrador current dominates the temperature regime of the northwest Atlantic (Smith et al., 1937; Dunbar, 1951; Bailey and Hachey, 1951; Hachey et al., 1954). The inner (shoreward) portion of this current, characterized by frigid water (< 0°C) of Arctic origin, extends from the shoreline to the edge of the continental shelf. Since capelin, being a sub-arctic species, spend a good deal of their time in water of Labrador Current origin, geographical variations in the temperature structure of the Labrador Current should be reflected in their growth pattern. May et al., (1965) using the data of Templeman (1960, 1961, 1962; MS, 1963) have shown that the volume of the very cold water in the Labrador Current declines from north to south. As a consequence, there is a diminution of the influence of this current in the southern extremes of its path. The spawning

of capelin on the beaches is known to occur only within a restricted temperature range (5.5-10°C) Templeman (1948). In southern localities (i.e. Bay of Fundy) where the Labrador Current has a reduced influence, solar warming of the surface waters enables spawning to occur very early. In Labrador, however, the shoreward branch of the Labrador Current together with the reduced solar heat retards the warming of the surface waters upwards to 3 months later than in the Bay of Fundy. In addition, the delayed warming of the surface temperatures in the north restricts the duration of the feeding season so that not only are capelin later spawning in Labrador but the larvae have a shorter period in which to feed.

There have been many discussions in the literature regarding the influence of temperature as a controlling factor determining the final size obtained by an organism. Taylor (1958) observed "that the large size and long life span are often associated with the cooler temperatures of higher latitudes". Holt (1958) states that theoretically L_∞ should increase slowly with decreasing temperatures and that fish which approach their L_∞ rapidly, seemingly tend to have shorter lives than those which approach it at a slower

pace. On the other hand, Allee et. al. (1949) and Clarke (1954) observe that poikilothermous animals tend to be smaller in colder climates. May et. al. (1965) found the same correlation to exist between cod growth and temperature in the Canadian northwest Atlantic.

We have seen that the relationship between temperature and size in capelin of the Canadian area of the northwest Atlantic is characterized by an increase in maximum size and age with a decrease in temperature but there is a corresponding decrease in the rate at which the maximum size is attained. This is explained on the basis of an early maturation and subsequent retardation of growth of the fast-growing fish in the southern region as compared to a much greater age at first maturity in the Labrador region.

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VI REFERENCES

Allee, W.E., A.E. Emerson, O. Park, T. Park, and K.P. Schmidt. 1949. Principles of Animal Ecology. W.B. Saunders Co., Philadelphia and London. 837 p.

Bailey, W.B., and H.B. Hackey. 1951. The vertical temperature structure of the Labrador Current. Proc. Nova Scotia Inst. Sci., 22(4): 34-48.

Brown, M.E. 1957. The physiology of fishes. Vol. 1. Academic Press Inc., New York, pp 361-400.

Carlander, K.D. 1956. Fish growth rate studies: Techniques and role in surveys and management. Trans. 21st North American Wildlife Conf. No. 21, pp. 262-274.

Clarke, G.L. 1954. Elements of Ecology. John Wiley and Sons Inc., New York, 534 p.

DeBont, A.F. 1967. Some aspects of age and growth of fish in temperate and tropical waters. In The Biological Basis of Freshwater Fish Production. John Wiley and Sons Inc., New York. 495 pp.

Dunbar, M.J. 1951. Eastern Arctic waters. Bull. Fish. Res. Bd. Can., 88: 1-131.

Dzin-Gi-Jun, and J. Popiel, 1961. Back-calculations of herring growth rate from scales and otoliths. Herring Commission 114, Conseil Perm. Int. Exploration Mer, C.M. 1961 (Mimeographed report).

Hachey, H.B., F. Hermann, and W.B. Bailey. 1954. The waters of the ICNAF convention area. Ann. Proc. Int. Comm. Northw. Atlant. Fish., 4: 67-102.

Hansen, P.M. 1943. Capelin (Mallotus villosus). Ann. Biol., 1: 121-124, Conseil Int. Expl. Mer.

Hempel, G. 1959. Growth of the otoliths of young herring. Helgol. Wiss. Meeresunters. 6: 3, 241-259. English Translation No. 613, Dept. Agr. and Fish., Mar. Lab. Aberdeen.

Hickling, C.F. 1933. The natural history of the hake. U.K. Min. Agr. and Fish., Fish. Invest., Ser. 2, 13(2): 120 pp.

Hile, R. 1936. Age and growth of the cisco, Leucichthys artedi in the lakes of the northeastern highlands, Wisconsin. Bull. U.S. Bur. Fish., 48: 211-317.

Holt, S.J. 1959. Water temperature and cod growth rate. Conseil Perm. Int. Exploration Mer, J. Cons., 24(2): 374-376.

Jeffers. G.W. MS, 1931. The life history of the capelin, Mallotus villosus (O.F. Müller). Ph.d. thesis Univ. of Toronto. 1-86 p.

Jones, J.W., and H.B. Hynes. 1950. The age and growth of Gasterosteus aculeatus, Pygosteus pungitius and Spinachia vulgaris as shown by their otoliths. J. Animal Ecol. 19(1): 59-73.

Jones, R. 1958. Lee's phenomenon of apparent change in growth rate with particular reference to haddock and plaice. Int. Comm. Northwest Atlantic Fish., special pub. No. 1: 229-242.

1962. Haddock bionomics. II. The growth of haddock in the North Sea and at Faroe. Scotland Dept. Agr. and Fish., Mer. Res. 1962, (2): 1-19.

Kanneworff, P. 1968. Preliminary results and some problems concerning capelin investigations at Greenland. Rapp. Procés-verbaux Réunions Cons. Perm. Int. Explor. Mer, 158: 38-40.

Kohler, A.C. 1964. Variations in the growth of Atlantic cod. J. Fish. Res. Bd. Canada 21(1): 41-60.

May, A.W. 1967. Otolith age validation in Labrador cod. Int. Comm. Northwest Atlantic Fish., Res. Bull. No. 4: 116-120.

May, A.W., A.T. Pinhorn, R. Wells and A.M. Fleming. 1965. Cod growth and temperature in the Newfoundland area. Int. Comm. Northwest Atlantic Fish., special pub. No. 6: 545-555.

Menon, M.D. 1950. Bionomics of the poor-cod Gadus minutus in the Plymouth area. J. Mar. Biol. Ass. U.K., Vol. 24(1).

Mina, M.V. 1968. A note on a problem in the visual qualitative evaluation of otolith zones. J. Cons. Perm. Int. Explor. Mar, 32(1): 93-97.

Mio, S. 1966. The determination of the age and growth of Gnathagnus elongatus. Bull. Jap. Sea Regional Fish. Res. Lab. No. 16: 1-6.

Pitt, T.K. 1958a. Age and growth of the capelin, Mallotus villosus from Newfoundland and Grand Bank areas. J. Fish. Res. Bd. Canada, 15(3): 295-311.

1958b. Distribution, spawning and racial studies of the capelin (Mallotus villosus) in the offshore Newfoundland area. Ibid., 15(3): 275-293.

Prokhorov, V.S. 1960. Post-spawning survival of the Barents Sea capelin (Mallotus villosus villosus - Müller). Conseil Perm. Int. Exploration Mer, Distant Northern Seas Committee No. 165, C.M. 1960.

Runnstrøm, S. 1936. A study on the life history and migration of the Norwegian spring-herring. Rept. Norwegian Fish. and Mar. Invest., Vol. 5, No. 2.

Saetersdal, G.S. 1953. The haddock in Norwegian waters II. Methods in age and growth investigations. Ibid., 10(9): 1-46.

Scott, D.M. 1954. A comparative study of yellowtail flounder from three Atlantic areas. J. Fish. Res. Bd. Canada, 11(3): 171-197.

Smith, E.H., F.M. Soule, and O. Mosby. 1937. The Marion and General Greene Expeditions to Davis Strait and Labrador Sea. Scientific Results, Part 2. U.S. Treas. Dept., Coast Guard Bull., 19: 1-259.

Sjöblom, V. 1963. Back calculation of the length of Baltic herring from measurements of the otolith. Institute of Mar. Res. Helsinki, Finland. Arch. Soc. Vanamo. 17(2). pp. 63-67.

Sleggs, G.F. 1933. Observations upon the economic biology of the capelin Mallotus villosus. Rept. Nfld. Fish. Res. Comm., 1(3) 65 pp.

Smith, H. 1956. Life history of the lake herring of Green Bay, Michigan. U.S. Fish. and Wildlife Ser., Fish. Bull. 109. Vol. 57.

Southward, G.M. 1962. A method of calculating body lengths from otolith measurements for Pacific halibut and its applications to Portlock-Albatross grounds data between 1935 and 1957. J. Fish. Res. Bd. Can. 19(2): 339-361.

Tait, J.B. 1952. Hydrography in relation to fisheries. Edward Arnold and Co., London. 106 p.

Taylor, C.C. 1958. Cod growth and temperature. Conseil Perm. Exploration Mer, J. Cons., 23(3): 366-370.

Tibbo, N., and R.D. Humphreys. 1966. An occurrence of capelin (Mallotus villosus) in the Bay of Fundy. J. Fish. Res. Bd. Can. 23(3): 463-467.

Templeman, W. 1948. The life history of the capelin Mallotus villosus (Müller) in Newfoundland waters. Res. Bull. No. 17, Newfoundland Govt. Lab., 151 pp.

1960. Canadian research report, 1959. A. Subareas 2 and 3. Ann. Proc. Int. Comm. Northwest Atlantic Fish., 10: 19-25.

1961. Canadian research report, 1960. A. Subareas 2 and 3. Ibid., 11: 23-31.

1962. Canadian research report 1961. A. Subareas 2 and 3. Int. Comm. Northwest Atlantic Fish., Redbook, Part II: 3-20.

MS, 1963. Canadian research report, 1962. A. Subareas 2 and 3. Ann. Meet. Int. Comm. Northwest Atlantic Fish., Doc. No. 13, Serial No. 1080.

1968. Review of some aspects of capelin biology in the Canadian area of the northwest Atlantic. Rapp. Procés-verbaux Reunions, Cons. perm. int. Explor. Mer, 158: 41-53.

Templeman, W., and H.J. Squires. 1956. Relationship of otolith lengths and otolith weights in the haddock Melanogrammus aeglefinus (L.) to the rate of growth of the fish. J.

Fish. Res. Bd. Canada, Vol. 13(4): 467-487.

Van Oosten, J. 1929. Life history of the lake herring Leucichthys artedi of Lake Huron as revealed by its scales, with a critique of the scale method. Bull. U.S. Bur. Fish., 44: 265-448.

Watkins, E.E. 1927. Investigation on Cardigan Bay herring. Rept. Mar. and Freshwater Invest., Dept. Zool. Univ. Coll. Wales. Vol. I-II, 1925-1927.

Winters, G.H. MS, 1966. Contribution to the life history of the capelin Mallotus villosus, in Newfoundland waters. Fish. Res. Bd. Canada, Mans. Rept. Ser. No. 870, 56 pp.

1968. Fishery investigation and groundfish landings. Fish. Res. Bd. Canada Circ. No. 15, pp. 17-23.

Zamakhaev, D.F. 1965. On the question of the effect of growth during the first years of a fish's life on its subsequent growth. Trudy Vsesoiuznogo Nauchno-issledovatel'skogo Instituta Morskogo Rybnogo Knoziaistva i Okeanografii (VINRO), Vol. 50, pp. 109-141, 1964. Fish. Res. Bd. Canada. Trans. Ser. No. 549, 48 p.

Table I. Origin of capelin samples used in this study.

Area	Locality	Number of specimens			
		Male	Female	Unsexed	Total
NE Labrador	Davis Inlet	38	75	-	113
Eastern Labrador	Pack's Harbour	150	150	-	300
Southern Labrador	Henley Harbour	104	116	-	720
Eastern Nfld.	Trinity Bay	505	465	198	1168
" "	Outer Cove	450	205	-	655
Grand Bank	SE Shoal, and Eastern Slope	470	480	-	950
Southern Nfld.	Grand Beach	125	100	-	225
Bay of Fundy	Passamaquoddy Bay to Lepreau	176	154	-	330

Table II. Back-calculated lengths of Trinity Bay capelin using the regression equations established for each age, sex and maturity. Lengths marked with an asterisk are back-calculated using the regression equation of mature 3-year-old capelin. Assuming immaturity at age 3, the lengths are 14.90 (M), 13.88 (F) age 4; 13.92 (M), 13.13 (F) age 5; 13.61 (M), 12.25 (F) age 6.

Age	Maturity	Sex	Back-calculated lengths (cm)				
			l_1	l_2	l_3	l_4	l_5
1	Imm	Juv	7.11				
2	Imm	M	7.43	11.48			
		F	7.23	10.96			
3	Imm	M	6.87	11.22	14.20		
		F	6.65	10.41	12.78		
3	Mat	M	7.93	12.85	18.15		
		F	7.57	11.73	15.86		
4	Mat	M	7.32	11.72	16.76*	20.08	
		F	7.12	11.17	15.37*	17.58	
5	Mat	M	6.74	11.05	15.29*	19.52	20.20
		F	6.83	10.76	14.11*	16.98	18.24
6	Mat	M	6.57	10.91	14.83*	19.43	20.02
		F	6.66	9.96	12.68*	16.00	17.98

Table III. Otolith radii (in EPU) of Trinity Bay capelin measured to the end of each winter zone for the various ages represented.

Age	Maturity	Sex	Radius of otolith (EPU)					
			R_1	R_2	R_3	R_4	R_4	R_6
1	Imm	Juv	8.17					
2	Imm	M	8.75	18.85				
		F	8.38	17.98				
3	Imm	M	7.73	18.24	23.88			
		F	7.32	16.52	21.60			
3	Mat	M	9.72	22.12	28.15			
		F	9.02	20.01	25.37			
4	Mat	M	8.55	19.44	25.74	29.99		
		F	8.18	18.52	24.58	27.73		
5	Mat	M	7.49	17.84	23.12	27.41	30.86	
		F	7.64	17.71	22.50	26.28	28.44	
6	Mat	M	7.16	17.49	22.32	27.00	30.50	32.00
		F	7.33	15.33	20.16	23.87	26.87	29.29

Table IV. Subsequent growth of male capelin in relation to their length at the end of the first year, Trinity Bay, March 5 - June 14, 1967. Lengths marked with an asterisk have been back-calculated using the regression equation of immature 3-year-olds.

Size Group (cm)	Length (cm) at end of age					Length increments (cm) at age				
	1	2	3	4	5	1	2	3	4	5
Age 3 (imm)										
5.94	5.94	10.53	13.60			5.94	4.59	3.07		
6.48	6.48	10.78	13.91			6.48	4.30	3.13		
7.02	7.02	11.29	14.06			7.02	4.27	2.77		
7.56	7.56	11.88	14.63			7.56	4.32	2.75		
Age 3 (mat)										
6.48	6.48	11.41	17.04			6.48	4.93	5.63		
7.02	7.02	12.17	17.56			7.02	5.15	5.39		
7.56	7.56	12.59	17.84			7.56	5.03	5.25		
8.10	8.10	12.93	18.18			8.10	4.83	5.25		
8.64	8.64	13.26	18.64			8.64	4.62	5.38		
Age 4 (mat)										
5.94	5.94	10.70	14.25* 15.79	19.80		5.94	4.76	3.55* 5.09	5.55* 4.01	
6.48	6.48	11.33	14.52* 16.19	19.89		6.48	4.85	3.19* 4.86	5.37* 3.70	
7.02	7.02	11.37	14.67 16.42	19.96		7.02	4.35	3.30* 5.05	5.29* 3.54	
7.56	7.56	11.38	14.85 16.70	19.99		7.56	3.82	3.47* 5.32	5.13* 3.28	
8.10	8.10	12.13	15.20* 17.22	20.18		8.10	4.03	3.03* 5.09	4.98* 2.96	
Age 5 (mat)										
5.40	5.40	10.28	13.49 14.65	19.38	20.07	5.40	4.88	3.21* 4.37	5.89* 4.37	0.69
5.94	5.94	10.76	13.78 15.08	19.50	20.22	5.94	4.82	3.02* 4.32	5.72* 4.42	0.72
6.48	6.48	10.91	13.81 15.12	19.47	20.19	6.48	4.43	2.90* 4.21	5.66* 4.35	0.72
7.02	7.02	11.20	14.03 15.45	19.52	20.21	7.02	4.18	2.83* 4.25	5.49* 4.07	0.69
7.56	7.56	11.19	13.91 15.28	19.50	20.13	7.56	3.63	2.72* 4.09	5.59* 4.22	0.63

Table V. Subsequent growth of female capelin in relation to their length at the end of the first year. Lengths marked with an asterisk have been back-calculated using the regression equation of immature 3-year-olds.

Size Group (cm)	Length (cm) at end of age					Length increments (cm) at age				
	1	2	3	4	5	1	2	3	4	5
Age 3 (imm)										
5.94	5.94	10.10	12.86			5.94	4.16	2.76		
6.48	6.48	10.36	12.71			6.48	3.88	2.35		
7.02	7.02	10.86	13.00			7.02	3.84	2.14		
7.56	7.56	10.40	12.75			7.56	2.84	2.35		
Age 3 (mat)										
6.48	6.48	10.89	15.20			6.48	4.41	4.31		
7.02	7.02	11.50	15.45			7.02	4.48	3.95		
7.56	7.56	11.62	15.69			7.56	4.06	4.07		
8.10	8.10	12.19	16.30			8.10	4.09	4.11		
Age 4 (mat)										
5.94	5.94	10.40	13.60* 14.90	17.23		5.94	4.46	3.20* 4.50	3.63* 2.33	
6.48	6.48	10.78	13.78* 15.20	17.49		6.48	4.30	3.00* 4.42	3.71* 2.29	
7.02	7.02	10.89	13.56* 14.84	17.49		7.02	3.87	2.67* 3.95	2.93* 2.65	
7.56	7.56	11.50	14.00* 15.57	17.65		7.56	3.94	2.50* 4.07	3.65* 2.08	
8.10	8.10	12.00	14.60* 16.55	18.10		8.10	3.90	2.60* 4.55	3.50* 1.55	
Age 5 (mat)										
5.94	5.94	10.59	12.86* 13.69	16.74	18.18	5.94	4.65	2.27* 3.10	3.86* 3.05	1.44
6.48	6.48	10.64	12.90* 13.75	16.71	18.15	6.48	4.26	2.26* 3.11	3.81* 2.96	1.44
7.02	7.02	10.86	13.20* 14.25	17.08	18.26	7.02	3.84	2.34* 3.39	3.88* 2.83	1.18
7.56	7.56	11.41	13.48* 14.70	17.36	18.40	7.56	3.85	2.07* 3.29	3.88* 2.66	1.04
8.10	8.10	11.81	13.79* 15.22	17.46	18.43	8.10	3.71	1.98* 2.65	3.67* 2.24	0.97

Table VI. Arithmetic regression equations of fish length on otolith radius for the various localities.

Area	Age	Maturity	Regression equation of fish length on otolith radius	
			Males	Females
Pack's Harbour	4	Mat	Y = 0.30X + 10.54	Y = 0.64X + 0.43
	5	Mat	Y = 0.21X + 13.35	Y = 0.28X + 10.00
Henley Harbour	2	Imm	Y = 0.43X + 3.68	Y = 0.44X + 3.37
Trinity Bay	1	Imm	Y = 0.54X + 2.70	Y = 0.54X + 2.70
	2	Imm	Y = 0.42X + 3.56	Y = 0.38X + 4.13
	3	Imm	Y = 0.38X + 5.13	Y = 0.37X + 4.79
	3	Mat	Y = 0.57X + 2.11	Y = 0.61X + 0.38
	4	Mat	Y = 0.22X + 13.49	Y = 0.41 + 6.21
	5	Mat	Y = 0.21X + 13.72	Y = 0.17X + 13.41
Outer Cove	3	Mat	Y = 0.28X + 10.20	Y = 0.35X + 7.06
	4	Mat	Y = 0.39X + 7.33	Y = 0.41X + 5.61
	5	Mat	Y = 0.25X + 11.92	Y = 0.33X + 8.33
Grand Bank	3	Mat	Y = 0.37X + 7.63	Y = 0.32X + 8.04
June 1967	4	Mat	Y = 0.31X + 9.63	Y = 0.35X + 7.43
	5	Mat		Y = 0.23X + 11.34
Grand Bank	2	Mat	Y = 0.22X + 10.04	Y = 0.35X + 5.77
Aug. 1967	3	Mat	Y = 0.42X + 5.65	Y = 0.31X + 7.67
	4	Mat	Y = 0.41X + 6.60	Y = 0.38X + 6.44
Grand Beach	3	Mat	Y = 0.26X + 10.33	Y = 0.17X + 11.09
	4	Mat	Y = 0.34X + 8.79	Y = 0.35X + 7.22
Bay of Fundy	3	Mat	Y = 0.25X + 15.01	Y = 0.38X + 5.08
	4	Mat	Y = 0.15X + 11.73	Y = 0.28X + 8.01

Table VII. Ratio of otolith radius (in EPU) to total length (in cm) of mature female capelin from the various localities.

	Ratio of otolith radius (EPU) to length (cm)					
Area	Bay of Fundy	Grand Beach	Grand Bank	Trinity Bay	Outer Cove	Pack's Harbour
12.0	1.73					
12.5	1.74					
13.0	1.72		1.68			
13.5	1.68	1.66	1.63			
14.0	1.67	1.63	1.68		1.71	
14.5	1.71	1.63	1.68	1.71	1.66	
15.0	1.69	1.65	1.67	1.67	1.59	
15.5	1.59	1.63	1.66	1.67	1.65	1.55
16.0	1.64	1.56	1.61	1.63	1.60	1.58
16.5		1.56	1.61	1.60	1.58	1.59
17.0		1.52	1.61	1.63	1.59	1.60
17.5		1.57	1.61	1.58	1.54	1.57
18.0		1.54	1.61	1.57	1.64	1.65
18.5			1.55	1.50	1.59	1.58
19.0			1.55	1.53	1.54	1.55
19.5				1.51		1.54
20.0				1.53		1.65
						1.54

Table VIII. Ratio of otolith radius (in EPU) to total length (in cm) of mature male capelin for various localities. True ratios may be obtained from the above ratios by dividing by 26.5.

Length (cm)	Ratio of otolith radius (EPU) to length (cm)					
	Bay of Fundy	Grand Beach	Grand Bank	Trinity Bay	Outer Cove	Pack's Harbour
12.0						
12.5						
13.0	1.72		1.69			
13.5	1.70		-			
14.0	1.71		1.62			
14.5	1.72		1.70			
15.0	1.69		1.63			
15.5	1.68	1.51	1.63		1.61	
16.0	1.68	1.55	1.68		1.66	
16.5	1.60	1.56	1.58	1.67	1.64	
17.0		1.57	1.60	1.68	1.65	1.59
17.5		1.54	1.63	1.54	1.60	1.49
18.0		1.58	1.61	1.57	1.58	1.52
18.5		1.53	1.59	1.52	1.62	1.53
19.0		1.54	1.54	1.51	1.58	1.51
19.5		1.51	1.56	1.56	1.55	1.57
20.0		1.55	1.48	1.54	1.59	1.53
20.5			1.56	1.50	1.51	1.50
21.0			1.49	1.46	1.53	1.54
21.5				1.49		1.51

Table IX. Average length at age as back-calculated from the regression equations given in Table VI. Lengths marked with an asterisk represent immature capelin.

Area	Age 1		Age 2		Age 3		Age 4		Age 5		Age 6	
	M	F	M	F	M	F	M	F	M	F	M	F
Pack's Harbour						14.10	18.48	16.90	19.30	17.78	20.13	18.92
Henley Harbour			10.02*	9.40*	12.71*	11.70*						
Trinity Bay	7.11*	7.11*	11.48*	10.95*	18.15 14.20*	15.86 12.78*	20.08	17.58	20.20	18.24	20.50	18.30
Outer Cove					17.86	15.63	18.81	16.69	19.63	17.68	19.90	
Grand Bank 1966					17.89	16.33	19.11	17.78		18.82		19.25
Grand Bank Aug. 1967			15.04	13.23	17.24	15.27	18.44	16.60	19.45	16.98	20.35	
Grand Bank June 1967			13.45*	13.30	17.84	16.16	18.70	17.06	19.33	17.95		
Grand Beach				12.78	17.01	15.25	18.23	16.15	19.35	17.36		
Bay of Fundy				12.75	15.01	13.69	15.57	15.28				

Table X. Age composition of mature capelin from various localities in the Canadian northwest Atlantic. (A) males; (B) females.

Age	Percent at each age						
	1966-67 Pack's Harbour	1967 Trinity Bay	1967 Outer Cove	June '67 SE Shoal	Aug. '67 SE Shoal	1966 Grand Beach	1966-67 Bay of Fundy
(A)							
2	-	-	-	-	27.4	-	-
3	0.6	23.0	38.7	76.6	50.0	47.7	58.5
4	36.3	52.3	48.1	21.8	17.9	52.3	41.5
5	55.0	22.8	13.1	1.6	3.5	-	-
6	8.1	1.9	0.1	-	1.2	-	-
Av. Age	4.71	4.04	3.75	3.25	3.01	3.52	3.42
(B)							
2	-	-	-	1.5	12.3	4.8	5.2
3	3.4	17.3	48.3	54.6	72.1	69.5	81.8
4	27.6	24.6	22.7	26.8	12.3	24.8	13.0
5	52.8	56.9	29.0	17.1	3.2	1.0	-
6	16.2	1.2	-	-	-	-	-
Av. Age	4.82	4.42	3.90	3.60	3.06	3.22	3.08